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16. ABSTRACT

This report describes two separate but interrelated substudies: an update of the macroecosystem model of the North Inlet Estuary near Georgetown, SC and a continuing study of experimental salt-marsh microecosystems. The model is under development to help understand the interactions of various parts of a natural ecosystem. The principal objective of the study is to develop and test replicate experimental salt-marsh units at the microecosystem level as diagnostic tools for assessing long- and short-term pollution effects on the Spartina alterniflora salt-marsh community.

Because of the complexity, this study was conceived as a five-year work. A summary of the first phase was published in the Ecological Research Series (EPA-600/3-77-016, January 1977). The present summary covers subsequent two years of study, March 1, 1976 to February 28, 1978. This report was submitted in fulfillment of Grant No. R804407-01 by the University of South Carolina, F. John Vernberg, principal investigator, under the sponsorship of the U.S. Environmental Protection Agency.

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EPA-600/3-78-092
October 1978

THE DYNAMICS OF AN ESTUARY

AS A NATURAL ECOSYSTEM, II

by

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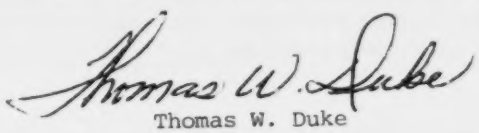
FOREWORD

The protection of our estuarine and coastal areas from damage caused by toxic organic pollutants requires that regulations restricting the introduction of these compounds into the environment be formulated on a sound scientific basis. Accurate information describing dose-response relationships for organisms and ecosystems under varying conditions is required. The EPA Environmental Research Laboratory, Gulf Breeze, contributes to this information through research programs aimed at determining:

- the effects of toxic organic pollutants on individual species and communities of organisms;
- the effects of toxic organics on ecosystem processes and components;
- the significance of chemical carcinogens in the estuarine and marine environments.

If we are to understand effects of pollutants, it is important to know how unstressed ecosystems function. This paper describes the basic structure and function of North Inlet Estuary, a large, relatively unpolluted salt marsh in South Carolina. The work was designed to prepare a general data base for future studies in polluted ecosystems. Concepts and generalizations given here may be of help in planning and interpreting field data.



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ABSTRACT

Although estuaries and marshlands are valuable as a natural resource, integrative scientific studies leading to the development of predictive models are practically nonexistent. Such studies are necessary for effective pollution control and long-term management of the estuarine ecosystem.

A research program was initiated to understand the dynamics of a relatively undisturbed estuary-marshland ecosystem, the North Inlet Estuary, near Georgetown, South Carolina. Because of the relative complexity of this type of study, a five-year study was proposed; a summary of the first two years' work has been published in the Ecological Research Series (EPA-600/3-77-016, January 1977). The present summary covers the next two years of study.

This investigation consists of two separate but interrelated substudies: an update of the macroecosystem model of the North Inlet Estuary and a continuing study of experimental salt marsh microecosystems. The model is being developed to help understand the interactions of various parts of a natural ecosystem. The principal objective of the microecosystem study was to develop and test replicate experimental salt marsh units at the micro-ecosystem level as diagnostic tools for the assessment of both long- and short-term pollution effects on the Spartina alterniflora salt marsh community.

This report was submitted in fulfillment of Grant No. R 804407-01 by the University of South Carolina, F. John Vernberg, principal investigator, under the sponsorship of the U.S. Environmental Protection Agency. This report covers a period from March 1, 1976 to February 28, 1978.

CONTENTS

Foreword iii
Abstract iv
Figures vi
Tables vii
Appendix viii

1. Introduction 1
2. Conclusions 3
3. Recommendations 4
4. Review of Pertinent Estuarine Ecosystem Studies 5
5. Simulation Model of the Coupling of a Salt Marsh Ecosystem and the Estuarine Water Column (H. McKellar, K. Summers, and R. Bonnell). 7
6. Development of a Salt Marsh Microecosystem (W. Kitchens). . . 56
7. Summary of Report (F. J. Vernberg). 71

References 72

FIGURES

Number		Page
1	Conceptual bases for overall model development	8
2	Conceptual diagram of the present simulation model indicating the dynamic coupling of the salt marsh and water column	10
3	Oscillation driving forces of the simulation model	11
4	Energy circuit diagram of the salt marsh subsystem showing the inputs and interactions of sunlight and temperature as well as the internal exchanges.	13
5	Energy circuit diagram of the water column submodel showing inputs and interactions of sunlight (S), temperature (T), tidal mixing (REMIX) and organic concentrations in the coastal sea as well as internal exchanges among POM, DOM, and fish	16
6	Simulation response for major components of the salt marsh subsystem	20
7	Simulation response for major components of the water column subsystem.	22
8	Generalized conceptual model depicting nutrient flow pathways in the microecosystem.	58
9	Cross section of a tank microecosystem unit.	60
10	Schematic of seawater system	61
11	Schematic of air sampling system	63
12	Exemplary nutrient flux curves	68
13	Exemplary community metabolism curves.	69

TABLES

Number		Page
1	Estimates of Areal Coverage of Major Subsystem of the North Inlet Estuary.	9
2	Macrofauna	65
3	Total Meiofaunal Densities between Microecosystem and Control Site .	66

APPENDIX

Number		Page
	List of all Table Titles	23
A1		24
A2		25
A3		29
A4		55

SECTION 1

INTRODUCTION

The value to man of such natural resources as marshlands and estuaries is indisputable and has been stressed by numerous national reports. Estuaries and their surrounding marshlands have served as centers of population and are heavily utilized for industrial development, shipping, fishing, and recreation. Furthermore, such usage is destined to increase in the future, with the predictable result of increased competition for these limited natural resources. Estuaries have been exploited, resulting in varying degrees of environmental deterioration, the extreme being massive destruction of various species. Despite recognition that estuaries are not an unlimited resource, integrated scientific studies leading to the development of predictive models are practically non-existent. Such integrated studies, rather than isolated studies of individual species, are necessary for effective pollution control and long-term management of the estuarine ecosystem. In particular, production, energetics, and the mechanisms of various processes as influenced by environmental perturbation are poorly understood, although the knowledge of these factors has obvious economic and fundamental scientific value.

Great diversity in kinds and shapes of estuaries has been reported in the scientific literature (Vernberg, 1976) . However, estuaries typically have certain characteristics in common, such as tidal fluctuation, salinity changes, and high concentrations of nutrients. Differences between estuaries may be quantitative or qualitative, such as the amount of wetlands or the amount and types of human habitation bordering their shores. Therefore, it is important to develop and compare ecosystem-oriented models of the major estuarine types if we are to assess the universal nature and differences of estuarine dynamics.

This study was undertaken to understand the ecosystem dynamics of a relatively undisturbed estuary, the North Inlet Estuary, near Georgetown, South Carolina. This report describes the third year study of what was designed to be a five-year project. After the project began, the study was expanded to include a specific section on a microecosystem.

This study consisted of two separate but interrelated substudies, that of the macroecosystem, and that of the microecosystem. For purposes of clarity, objectives are presented separately.

SECTION 2

CONCLUSIONS

Results in the third year of a proposed five-year analysis of a relatively undisturbed marsh-estuarine ecosystem have included an update and simulation studies of an energy flow model and more detailed investigation of the applicability of a microecosystem for assessing environmental perturbation. Because of budget cuts, no additional field data necessary for model development were collected. The technology to use a new bioassay tool, a salt-marsh microecosystem, was developed. However, additional work needs to be undertaken to test the system after environmental perturbation in order to evaluate the predictive capability of this method.

SECTION 3

RECOMMENDATIONS

Since this study was designed as a five-year project, definitive recommendations are premature. However, we suggest the following based on three years' experience:

1) The study of relatively undisturbed ecosystems is necessary to understand the dynamics of how systems work and to serve as a vital baseline with which to compare perturbed areas.

2) Since natural environmental units are complex and it takes time and effort to analyze them, it is recommended that granting agencies recognize the need for supporting long-term projects.

3) To realize the maximal return on the investment to develop a salt marsh microecosystem, this phase of the study should be continued in order to accomplish the stated research goals.

SECTION 4

REVIEW OF PERTINENT ESTUARINE ECOSYSTEM STUDIES

One of the first attempts to construct an energy flow diagram for an estuarine-marsh ecosystem was that of Teal (1962) for the marshes of Sapelo Island, Georgia. Teal proposed an energy flow diagram based on the data of various investigators. During one year, the input of solar energy was approximately 600,000 kcal/m^2. This energy was estimated to be partitioned as follows: most of the energy (93.9%) was dispersed as heat in photosynthetic activity, and 6.1% was converted to organic matter in gross primary production. After plant respiration, 1.4% of the incident light energy was left as net primary production. Of the energy available to secondary consumers, 55% was expended in respiration, while 45% of net production was exported. Since this study, more detailed energy budgets have been published for various individual species found in the estuarine-marsh ecosystem and other estuarine systems have been studied as described below.

Recently, a detailed study of a New England salt marsh was made by Nixon and Oviatt (1973). The two studies differed in that Teal emphasized energy flow in the marsh, while Nixon and Oviatt were concerned with energy flow in marsh creeks and embayments. Since consumption for the embayment exceeded production based on a yearly energy budget, this aquatic system must depend on input of energy in the form of organic detritus from marsh grasses. Production values of New England marsh grass were similar to those from New York, but markedly lower than those of southern marshes. This finding may reflect the substantial difference in climatic conditions between these geographical regions. Marked seasonal differences in energy flow patterns of New England ecosystems were observed. The flow of energy is much more complex and values are higher during summer than in winter. Thus, pollutants introduced at different times of the year might not only have a greater differential seasonal effect on northern marshes, but northern marshes might respond differently from those in southern regions.

In North Carolina the Newport River estuarine ecosystem is being studied by the Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, Beaufort, North Carolina.

An active program involving Georgia salt marshes has continued since the earlier work of Teal (1962), and recently Wiegert et al. (1975) presented a preliminary ecosystem model of a Georgia Spartina marsh. Pomeroy et al. are continuing studies on the intermediary metabolism of a salt marsh.

The dynamics of energy flow expressed as carbon in an estuarine-marsh

ecosystem, Barataria Bay, Louisiana, was described by Day et al. (1973). This study differs from the ones described above in that it deals in greater detail with all parts of the estuarine-marsh complex. Like other marshes, energy was available to be exported to the water, but unlike the findings of Nixon and Oviatt, a net community production in the water column was reported.

Vernberg et al. (1977) have described the North Inlet marsh-estuarine ecosystem using three sub-models: intertidal, benthic subtidal, and water column. A detailed example of the intertidal oyster subsystem of the intertidal submodel was described by Dame and Stevens (1977).

The report of the first two years of this proposed five-year study was published by the Environmental Protection Agency in the Ecological Research Series (Vernberg et al., 1977).

The present report is presented in two parts: 1) microecosystem studies, and 2) the North Inlet marsh-estuarine model.

SECTION 5

SIMULATION MODEL OF THE COUPLING OF A SALT MARSH ECOSYSTEM AND THE ESTUARINE WATER COLUMN

H. McKellar, K. Summers, and R. Bonnell

INTRODUCTION

The long-range purpose of the ecosystem modeling effort is to provide an overview of our evolving understanding of the North Inlet estuarine ecosystem. In doing so, we hope to formulate a simulation model which incorporates the major parts and processes which characterize southeastern salt marsh estuaries in general.

The conceptual base for the model development is illustrated in Figure 1. The fully developed model of the total estuarine system will incorporate inputs representing a wide spectrum of external forcing functions from terrestrial, atmospheric, and oceanic sources. Responses to inputs of sunlight and temperature are of primary concern, especially with respect to seasonal responses of biotic processes. The internal functioning of the model represents a dynamic exchange of energy and materials among several major subsystems as indicated in Figure 1. The intertidal subsystem is dominated by the Spartina salt marsh but also includes extensive mud flats and oyster reefs. The subtidal benthic subsystem is dominated by heterotrophic assemblages of macro- and meio-consumers. The water column subsystem is dominated biologically by planktonic organisms but also receives major inputs of energy and material from the contiguous marsh and underlying benthic systems. The energy and material within the water column also exchange with the sea and adjacent bays. This exchange takes place as a tidally driven passive transport of materials which are dissolved or suspended in the water mass as well as an active migration of nektonic organisms through the inlets. The areal coverage at mid-tide of all major subsystems has been estimated by planimetering existing maps of the region (Table 1).

Previous progress toward establishing the data base for the North Inlet estuary as well as the initial development of linear subsystem models are presented earlier (Vernberg et al., 1977). We present in this report a nonlinear simulation model of the coupled interaction between the salt marsh and the estuarine water column subsystems. This model is driven externally by inputs representing seasonal oscillations of sunlight, temperature, and tidal mixing. The proposed structure and functional interactions of the system are described and the mathematical formulation is presented along with an appended

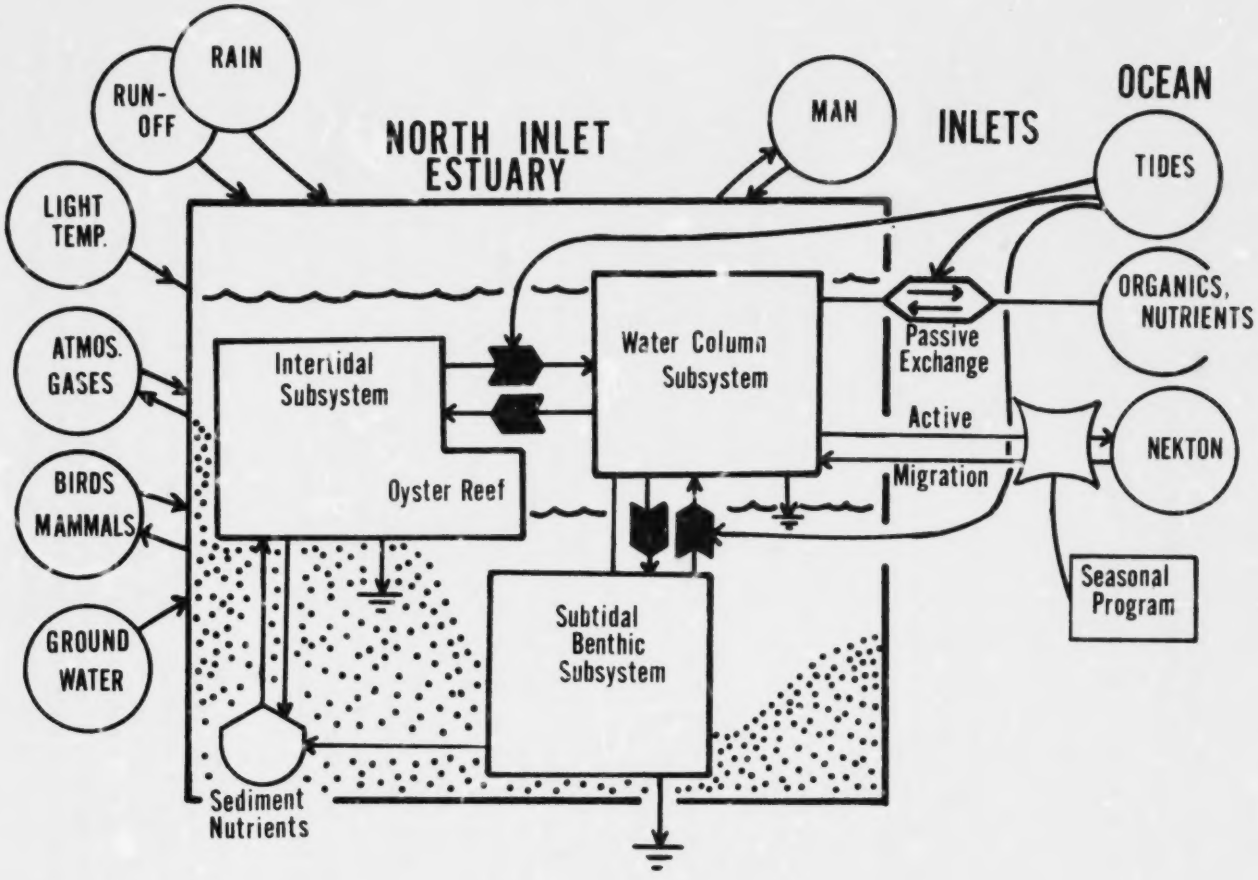


Figure 1. Conceptual bases for overall model development. External driving forces are indicated by the circle symbols and the internal subsystems are indicated by labeled boxes.

TABLE 1. ESTIMATES OF AREAL COVERAGE OF MAJOR SUBSYSTEM OF THE NORTH INLET ESTUARY

Subsystem	Symbol	Area (Hectares)
Intertidal		
Salt Marsh	A1	2513
Oyster Reefs	A3	137
Mud Flats	A5	82
Water Column	A2	709
Subtidal Benthic	A4	779

documentation of the necessary references, calculations, and assumptions. Simulation results are shown to indicate the seasonal behavior of the major components of the modeled system.

THE SIMULATION MODEL

The model, as thus far developed, represents the dynamics of organic matter in the coupled system of salt marsh and estuarine water mass. Organic exchange processes between the water column and the sea are also included. Figure 2 represents the conceptual status of this model as compared to the overall concept diagrammed in Figure 1. This model includes oscillating driving forces of sunlight, temperature, and tidal exchange. The simulated inputs from the oyster reefs and the subtidal benthic subsystems are included as constants since these subsystems have not yet been coupled as dynamic components of the model. The concentrations of dissolved and particulate organic matter in the coastal sea are also included as constants in these initial simulations.

The Driving Forces

The programmed inputs of the oscillating driving forces (Fig. 3) represent periodic changes which are critical to the seasonal behavior of organic exchange. The sunlight curve was programmed with data representing an eleven-year average for the South Carolina coast (Charleston) (U. S. Department of Commmerce, 1964).

The minimum and maximum water temperatures were programmed to lag 40 days behind the sunlight curve with an annual oscillation between 5°C and 30°C.

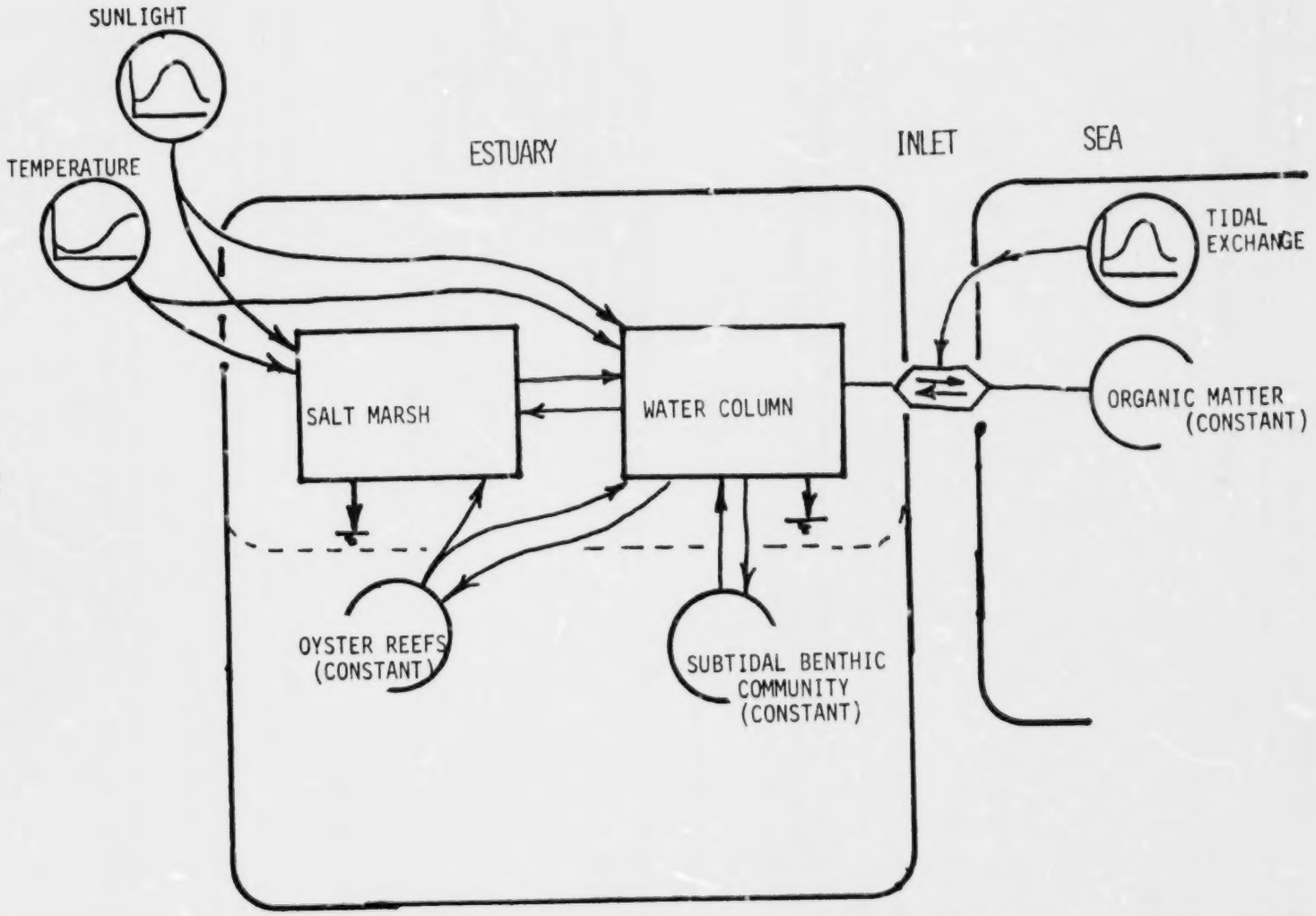


Figure 2. Conceptual diagram of the present simulation model indicating the dynamic coupling of the salt marsh and water column.

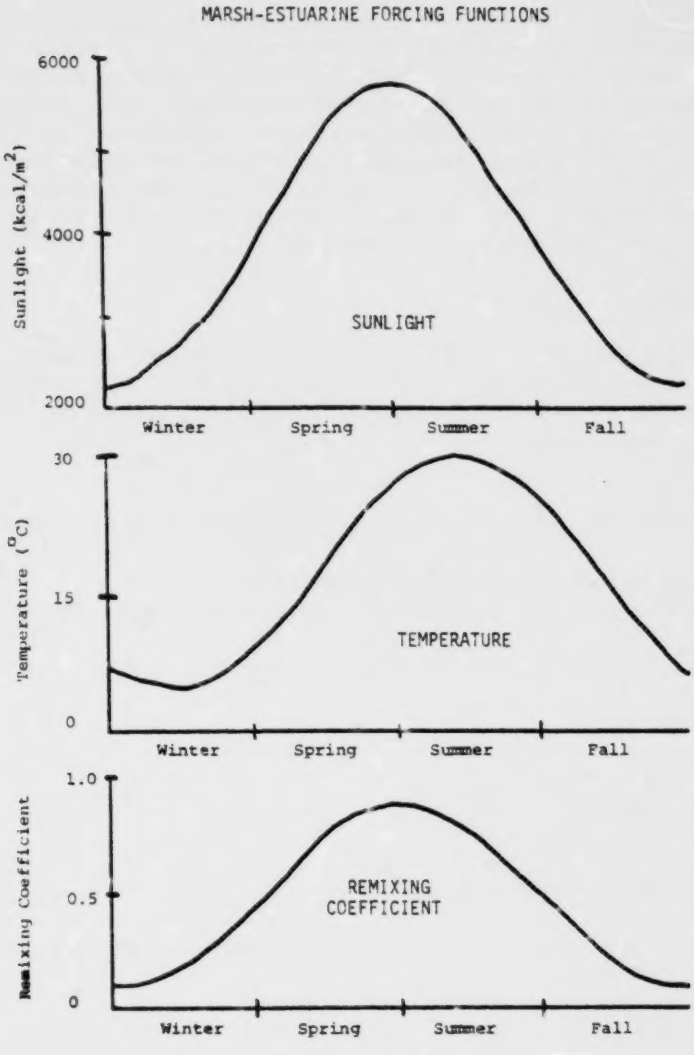


Figure 3. Oscillation driving forces of the simulation model.

SUNLIGHT = 3945 + 1695 (SINE(.0172 x TIME))
TEMPERATURE= 17.5 + 12.5 (SINE(.0172 x (TIME - 40))
REMIXING
COEFFICIENT= .5 + .4 (SINE(.0172 x TIME))

The tidal exchange characteristics include a "Remixing Coefficient" which represents the relative fraction of the ebb tide volume which reenters the estuary on the next flood tide. This function has significant consequences on the actual amount of net exchange of material with the coastal sea. For these simulations we examine the consequences of a sinusoidal fluctuation of the "Remixing Coefficient." This function was assumed to have a winter minimum of 10 percent reentry of the plume (when along-shore currents are strong and there are general turbulent conditions at the inlet) and a summer maximum of 90% (when along-shore currents are relatively weak and calm conditions exist at the inlet). These preliminary assumptions were based mainly on speculation and the actual behavior of this function is yet to be determined (B. Kjerfve, personal communication).

The Salt Marsh Submodel

The detailed structure and functional interactions of the salt marsh submodel are given as an energy flow diagram in Figure 4. The energy circuit symbols used here are consistent with those formalized by Odum (1971, 1972) (See Appendix, Table A1).

Structure--

The state variables of the submodel include three primary producers,

X_1, Spartina biomass, both above and below ground;
X_2, biomass of marsh algae on the mud surface below the Spartina; and
X_{14}, biomass of microbenthic algae on the mud flats

three marsh consumers,

X_4, macrofauna;
X_5, meiofauna; and
X_8, birds

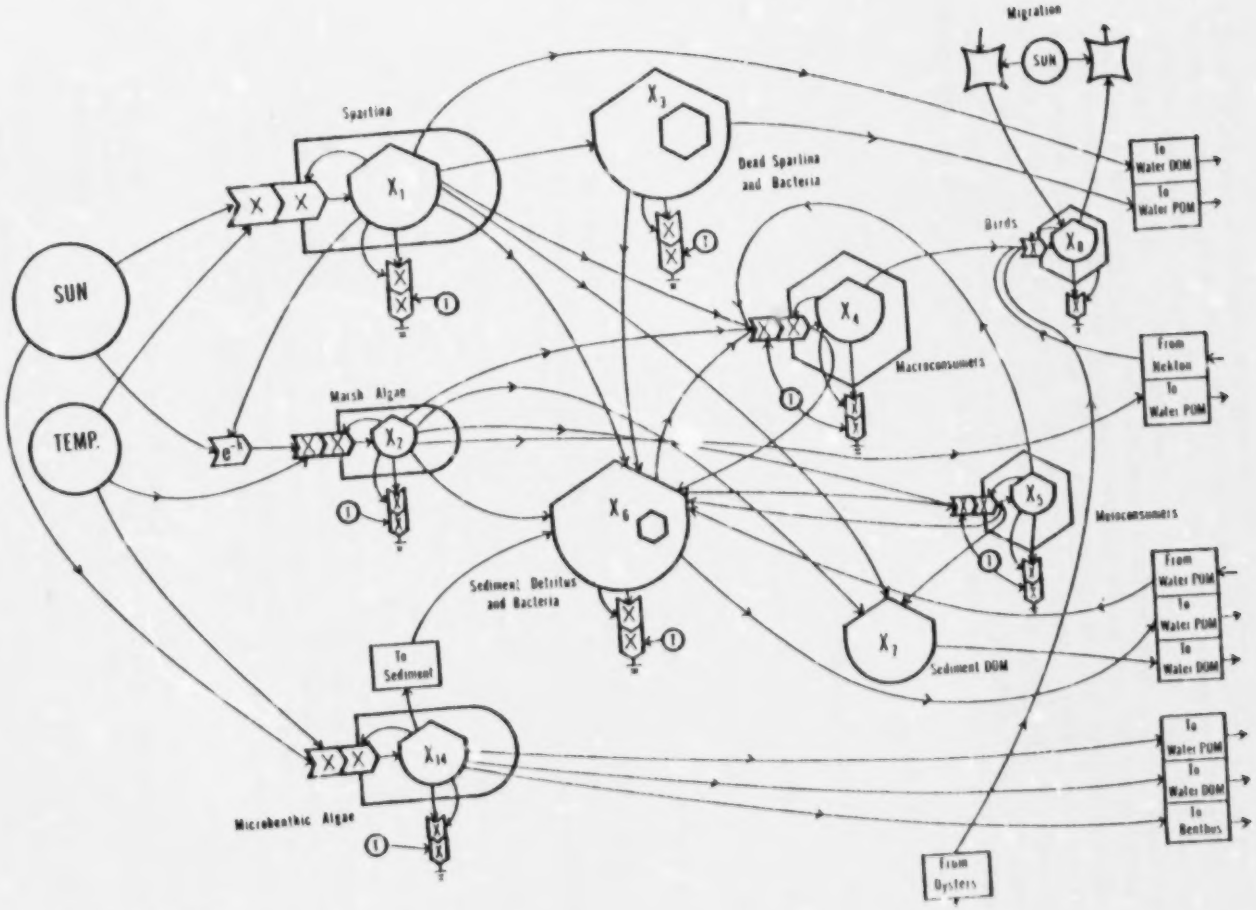
and three organic storage compartments,

X_3, above ground detritus representing mainly dead Spartina and attendant bacteria;
X_6, sediment detritus and attendant bacteria; and
X_7, dissolved organic matter (DOM) in the sediments.

Functioning--

The inputs of sunlight and temperature are considered as main driving forces for the model. These inputs control major systems functions of primary production, respiration, and trophic transfers. Pathways of energy transfer through the marsh include the major detrital pathways documented for marsh-estuarine sytems as well as direct grazing on producers by meio- and macro-consumers. The release of dissolved organic matter by all biotic compartments is also indicated.

The vertical row of boxes on the right of Figure 4 identify the major



MARSH SUBMODEL

Figure 4. Energy circuit diagram of the salt marsh subsystem showing the inputs and interactions of sunlight and temperature as well as the internal exchanges. The boxes on the right indicate pathways of exchange with other subsystems.

routes by which energy is exchanged with the adjacent water column, oyster reefs, and benthic subtidal systems.

The gross primary production of the energy in organic compounds by the salt marsh flora was considered to be directly proportional to the product of available sunlight, temperature, and producer biomass. (See Appendix, Table A2 for the complete mathematical representation of model functions.) For the marsh algae on the mud surface beneath the Spartina, the available sunlight is attenuated by the above ground Spartina biomass. There exists a definite shading effect of the Spartina on the marsh algae as documented by Van Raalte et al. (1976). We considered the attentuation of sunlight as it passes through the Spartina to be a general logarithmic extinction function of above ground Spartina biomass. Since X_1 in our model is total Spartina biomass, we assume that the above ground portion is 60% of the total so that

$$SS = (S)(e^{(-K8 \cdot AX_1)}$$

where S is the incident sunlight,

SS is the sunlight reaching the marsh algae,

K8 is the extinction coefficient, and

AX_1 is the above ground portion of $X_1 = (.6X_1)$.

The extinction coefficient (K8) was calculated fron data presented by Van Raalte et al. (1976) to be 0.0027. Thus, when Spartina biomass is high the percent transmission of sunlight to the algae is correspondingly low.

Respiration of each biotic compartment represents a loss of organic energy and is considered to be directly proportional to the product of water temperature and the square of the componert biomass. Thus, the effect of temperature on respiration is combined with a quadratic function of biomass representing a crowding effect of individuals within the compartment. Quadratic respiratory functions have been used by O'Neill (1976) in his general, 3-variable ecosystem model. Such functions for component respiration are not fully substantiated by measurements but seem to produce valid results in simulation models. All compartments in this submodel include this respiratory function except the dissolved organic matter in the sediment (DOM, X_7).

Trophic transfers of the energy in organic compounds among compartments are considered to be directly proportional to the product of the concentration of the food source, the biomass of the recipient, and water temperature.

The remaining exchanges of the energy in organic compounds described in this model are considered to be linear, donor controlled exchanges. The linear flows in this model include:

- release of dissolved organic matter by all biotic components,
- death rates of all biotic components (i.e., transfer of living biomass

to detritus-bacteria compartments (X_3 and X_6), and
- export flows from the marsh to the water column subsystem. Again, the vertical row of boxes on the right in Figure 4 identify the external subsystem components to which the energy is exported as well as the sources for energy import to the marsh from external components.

The imports of energy to the marsh from other subsystems include:

- food sources to the marsh birds from fish in the water column and from organisms of the oyster reefs,
- the settling of particulate detritus onto the marsh floor with flood tides.

The flow from oyster reef to marsh birds was evaluated and held constant in this model since the oyster reef component is not yet a dynamic part of the model.

The Water Column Submodel

Earlier development of a seven-compartment linear model of the water column subsystem for North Inlet was presented by Bonnell (1977). Compartments in this previous model have been aggregated into three functional units for coupling with the other submodels of the North Inlet ecosystem. In addition, several non-linear interactive terms have been specified. The present status of development of the water column subsystem is given in Figure 5.

Structure--

The three dynamic compartments in this submodel include:

- Particulate Organic Matter (X_9, POM), which represents an aggregation of phytoplankton, zooplankton, detritus, and bacteria,
- Dissolved Organic Matter (X_{10}, DOM), and
- Fish (X_{11}).

Future development of the water column model will perhaps include a separation of the living and non-living components of particulate organic matter. This separation may be necessary to fully address issues concerning the behavior of planktonic organisms as separate from detritus. However, at this stage of development, the model focuses more on the issues of total organic exchange rather than on the details of plankton dynamics.

Functioning--

The functional relationships of the water column subsystem are similar to those described for the salt marsh subsystem.

Gross primary production of organic energy in the water column represents an input to particulate organic matter. This function was considered to be directly proportional to the product of sunlight and temperature as indicated in Figure 5. Since much of the total POM is non-autotrophic, the positive feedback function of X_9 in controlling primary production was not included.

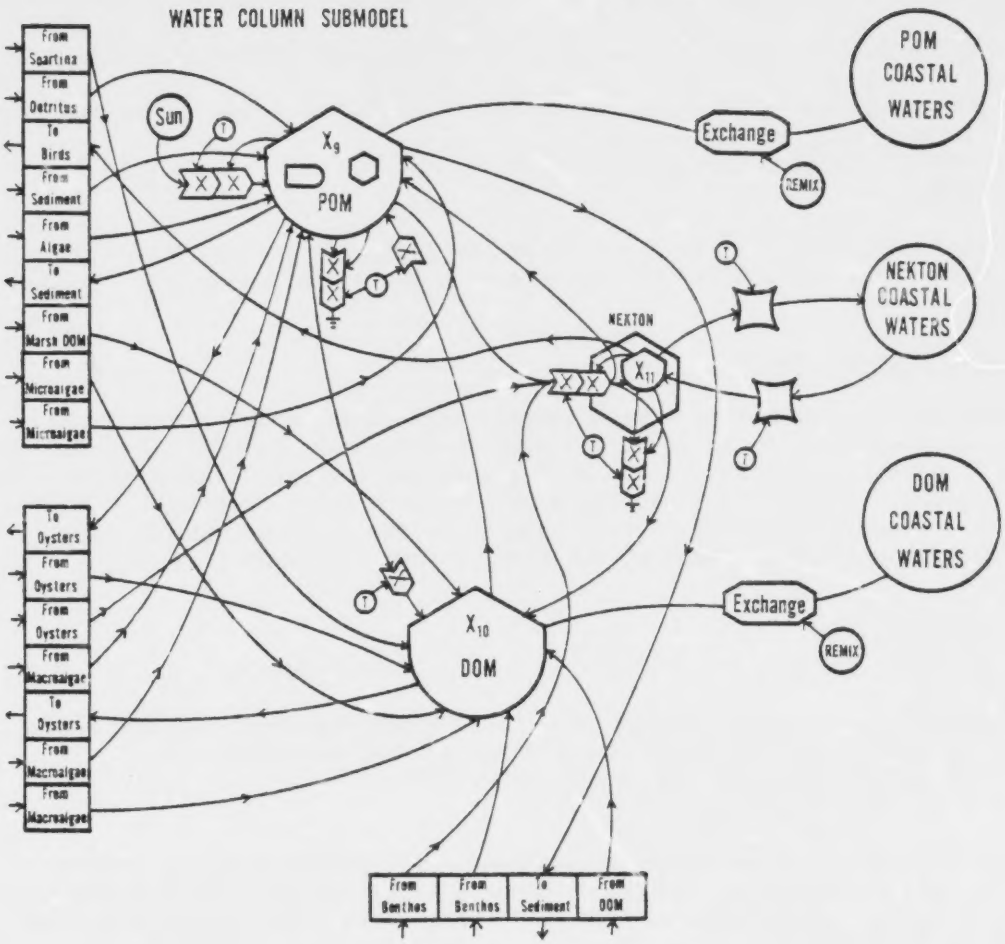


Figure 5. Energy circuit diagram of the water column submodel showing inputs and interactions of sunlight (S), temperature (T), tidal mixing (REMIX) and organic concentrations in the coastal sea as well as internal exchanges among POM, DOM, and fish. The boxes on the upper, lower, and left margins of the submodel indicate pathways of exchange with other subsystems.

Organic loss due to respiration is included for both POM and fish. Just as for the salt marsh subsystem, respiration was considered to be directly proportional to the product of temperature and the square of the biomass.

Trophic transfers in the water column are represented by the ingestion functions of the fishes. Ingestion rates are considered to be directly proportional to the product of the food source concentration, temperature, and the biomass of the fishes.

Planktonic release of DOM as documented by Hellebust (1965) is included in the model as a temperature-dependent flow from POM to DOM.

Planktonic uptake of DOM as documented and quantified by Crawford et al. (1974) is represented by a temperature dependent exchange from DOM to POM.

Release of organic matter by the fish due to egestion of particulate matter and the excretion of dissolved materials is included as temperature dependent flows from fish to POM and DOM.

Organic exchange with the coastal sea is indicated in Figure 5 by the "import-export" gates between the water column and the organic concentration in the sea. As a focal point of this study, we consider a net rate of exchange in the model which is directly proportional to the concentration gradient between the estuary and the sea. However, this net exchange is inhibited by the extent to which tidal remixing of the previous ebb-tide plume occurs (see "Remixing Coefficient", Fig. 3). Thus, a maximum rate of net exchange through the inlets would occur when tidal remixing is minimal (i.e., winter conditions) and when a large concentration gradient exists between the estuary and the sea. Mathematically stated

$$EX = K_{ex} (X-X_s)(1-REMIX)$$

where EX is the net rate of exchange through the inlet,

K_{ex} is a proportionality exchange coefficient,

X is the concentration of a dissolved or suspended organic fraction in the estuary,

X_s is the concentration of that fraction in the sea,

REMIX is the "Remixing Coefficient" as programmed in Figure 3.

This function for the exchange mechanism is a simplification of a very complex process. Complete functional analysis of the dynamics of exchange would require an extensive program of hydrodynamic sampling and modeling techniques which is beyond the scope of this study. However, we believe that the overall functioning of the exchange process between the estuary and the sea can be approximated in the way described above. Continued work will be directed toward refining this function in the model.

Mathematical Formulation

Differential Equations--

Explicit mathematical expressions for each energy flow pathway shown in Figures 4 and 5 were formulated as stated in the text. The terms representing input and output for each state variable were combined to describe the time rate of change for the model compartments. The resulting set of differential equations is listed in the Appendix (Table A2) as actual excerpts from the simulation program.

Energy Balance Factors--

The standing stocks of organic matter for each subsystem represented in the model were evaluated in terms of energy content (kcal) per square meter of each individual subsystem. Similarly, the exchange rates were evaluated in terms of kcal per m^2 of each subsystem per day. Thus, a mathematical expression representing flow from one subsystem to another must incorporate energy balance factors to account for the areal differences between subsystems. In effect, these energy balance factors are the ratios of the area of the "donor" subsystem to the area of the "recipient" subsystem. For example, consider an outflow of 1 kcal/m^2/day from a 2513 hectare salt marsh (Table 1) to a 709 hectare surface area of estuarine water. The inflow to the water mass would be 3.54 kcal/m^2/day (2513/709 = 3.54). In this way, the model conserves mass and energy at all transfers between modeled subsystems of varying areal coverage.

Evaluation of Coefficients--

In order to evaluate the coefficients for the model, a complete set of estimates for the standing stocks of model compartments and exchange rates were required. Much of the data needed to evaluate model parameters for the water column subsystem were collected from the North Inlet estuary as reported in Vernberg et al. (1977). Data from the North Inlet salt marsh is still being synthesized for incorporation into the model. However, for initial development of a functional salt marsh submodel we relied heavily on published data from other salt marshes along the east and Gulf coasts. This was necessary because there were not funds available in this grant for gathering data on the North Inlet except as reported by Vernberg et al. (1977). These data along with information generated from published laboratory experiments have provided an adequate quantitative base for the establishment of a functioning model. Detailed documentation of the data, calculations, and assumptions used in the evaluation of model parameters is given in the Appendix (Table A3). This documentation gives the initial conditions for the model compartments and flow rates which represent average annual conditions in the estuary.

Given this data base, the model coefficients were empirically determined. For example, the rate of gross primary production of Spartina (FO1) in the salt marsh subsystem was considered to be directly proportional to the product of sunlight (SUN), water temperature (TEMP), and existing Spartina biomass (Table A2). Mathematically,

$$FO1 = (K1)(SUN)(TEMP)(X1)$$

where K1 is the proportionality coefficient relating these parameters. Thus, with adequate estimates of gross production, sunlight, temperature, and biomass, the coefficient was then calculated as

$$K1 = \frac{FO1}{(SUN)(TEMP)(X1)}$$

A complete list of coefficient values used in the preliminary simulations is given in Table A4 in the Appendix.

Simulation Results

The model was programmed in CSMP-IV (Continuous System Modeling Program) which is a specialized computer program developed by IBM and tailored for the solution of systems of differential equations. The program was then simulated on an IBM 370/165 digital computer. The simulated time span started at the spring equinox (time when sunlight approximately equals the annual mean) and lasted for 1500 days (approximately 4 years) with output printed every 10 days. Beginning with output day 1010 (early winter of the third year) the computer output was translated by hand to graph paper and was plotted for an annual cycle.

The responses of the major compartments of the salt marsh subsystem (Fig. 6) show stable annual changes which resemble the annual fluctuations documented for several salt marsh systems (Nixon and Oviatt, 1973; Young, 1974; Kirby and Gosselink, 1976).

The simulated marsh community metabolism underwent a springtime surge up to an early summer maximum and a more gradual decline to low winter values. The integrated curves for daily metabolism yielded an annual primary production of around 33,500 kcal/m^2. Considering the slight increase in sunlight and temperature between South Carolina and Georgia, this value representing the North Inlet system compares favorably with the 36,380 kcal/m^2/yr documented for the Sapelo Island marsh (Teal, 1962). The simulated annual net production of organic matter was about 3000 kcal/m^2.

The *Spartina* compartment was the dominant simulated producer compartment of the model. The annual response showed a spring increase in biomass to an early summer maximum of about 2,700 kcal/m^2, followed by a gradual decline to a late winter maximum of around 700 kcal/m^2.

Above ground detritus, composed primarily of dead *Spartina* showed a phased lag response behind living *Spartina* biomass. This compartment showed a late spring increase to a rounded late summer and fall maximum followed by a gradual decline to a late winter, early spring minimum.

The largest organic storage compartment in the model was the sediment detritus and attendant bacteria. Output for this compartment was not plotted since it began with an initial stock of 1.75 x 10^5kcal/m^2 and remained relatively constant throughout the simulation. The absolute value dropped by less than 2% during the simulated four-year period.

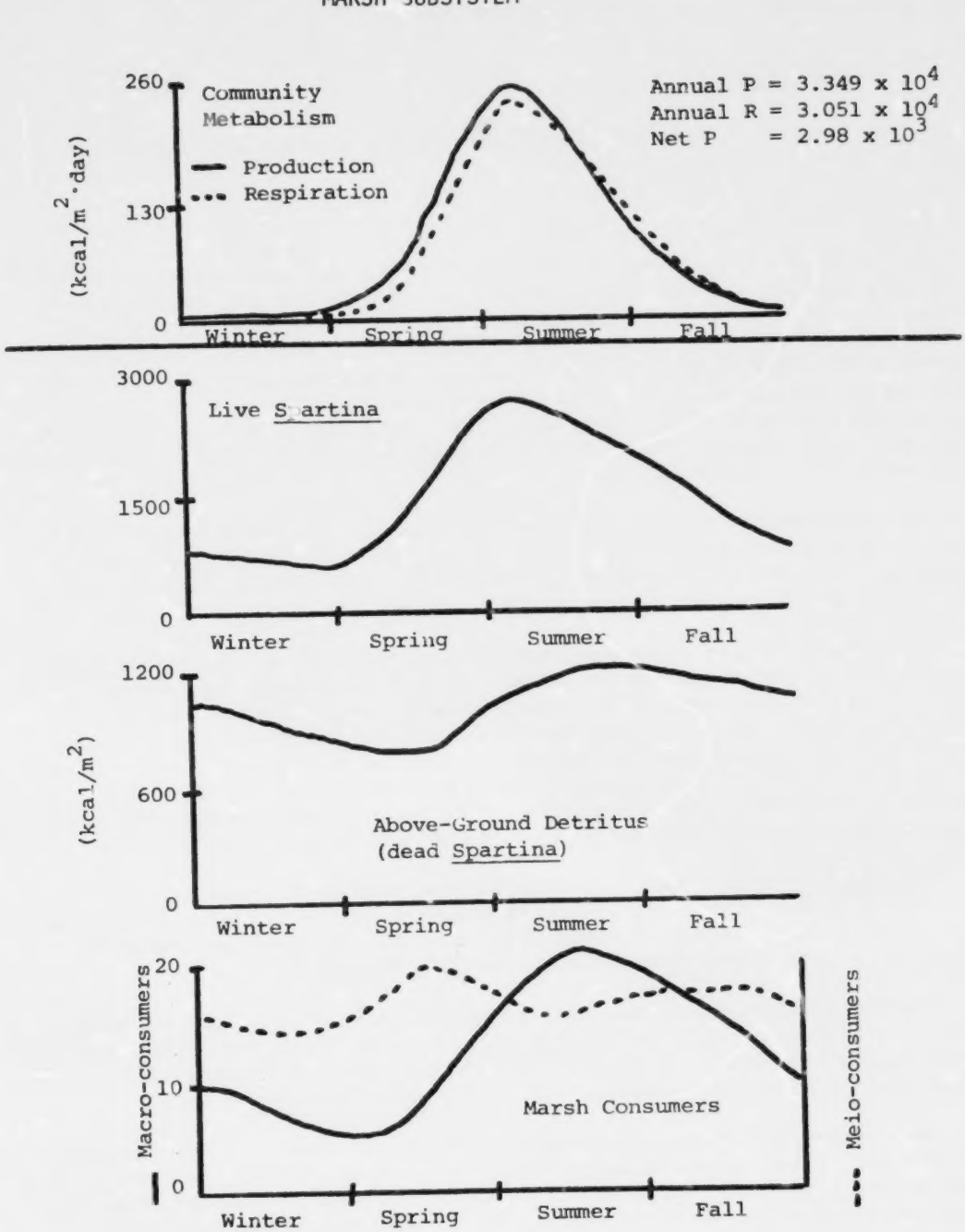


Figure 6. Simulation response for major components of the salt marsh subsystem.

The simulated macro-consumer biomass of the marsh, which in the field is composed primarily of the fiddler crab (Uca), showed an oscillation between an early spring minimum of 5-6 kcal/m^2 and a summer maximum of about 20 kcal/m^2. The meio-consumer biomass compartment, which was an order of magnitude less than the macro-consumers, showed a bi-modal oscillation with one sharp peak in the spring and an additional rounded peak over the late summer and fall.

Consistent with Teal's previous analysis of energy flow in the salt marsh (1962), this model incorporates a significant output of organic matter from the marsh to the estuarine water column. This organic load to the water column tends to stimulate heterotrophic growth and respiration (Odum, 1971; Wright and Hobbie, 1966). As a consequence, the model response for water column metabolism (Fig. 7) shows a general dominance of respiration over in situ production in the water. The model predicts an annual gross primary production in the water of about 6000 kcal per m^2 of water surface and an annual respiratory organic consumption of about 11,000 kcal/m^2.

The annual stock of simulated particulate organic matter in the water is relatively constant compared to the simulated fluctuation of dissolved organic matter. The DOM compartment reaches a summer peak which is more than 2 times higher than its winter minimum.

The remixing coefficient is shown again in Figure 7 to illustrate the relationship between organic concentration in the estuarine water, tidal remixing, and the resultant exchange with the coastal sea. According to the proposed relationships presently stipulated in the model, the simulated export rate of organic matter from the estuary is low during the summer, even though the organic concentration in the estuary is at its peak. This trend results because of the large portion of the ebb-tide plume which is speculated to reenter the estuary during subsequent flood tides during the summer, thus inhibiting the net exchange with the sea. Conversely, when turbulent conditions exist in the winter (tidal remixing is minimum) there is a maximum rate of simulated net export.

SUMMARY

A non-linear, deterministic model of the interactions within and between the Spartina salt marsh and the estuarine water mass has been proposed and simulated. Preliminary simulation results show that the modeled system is stable and produces seasonal changes in simulated parameters which resemble measured fluctuations in Spartina-dominated estuaries. Whether or not these simulated trends in metabolism, biomass, and export are actually characteristic of the North Inlet estuary will be determined by continued data analysis and collection. Regardless of the present validity of the model it represents, the status of our understanding of the North Inlet marsh-estuarine ecosystem with its complex interactions of physical, geochemical, and biological processes.

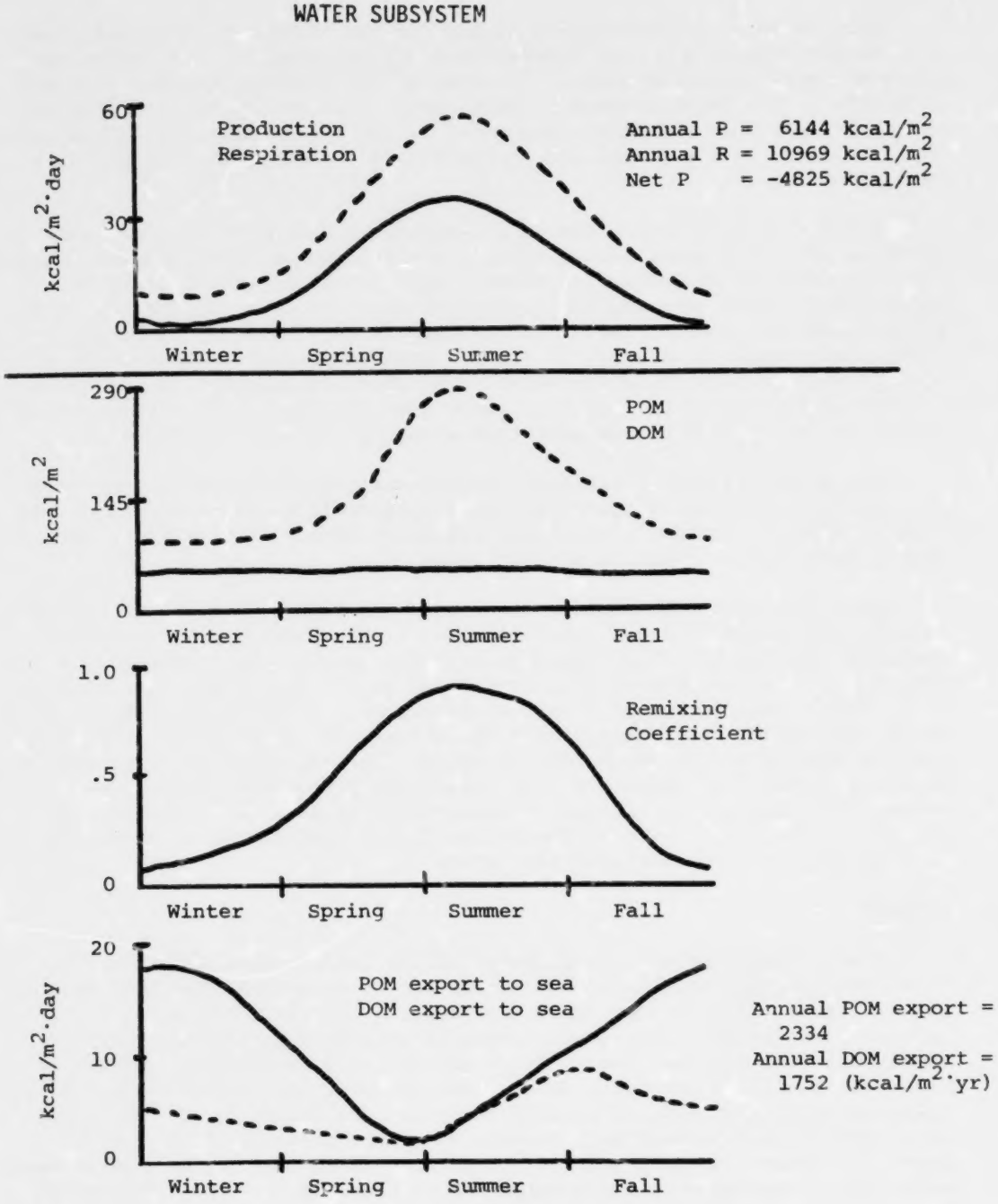


Figure 7. Simulation response for major components of the water column subsystem.

APPENDIX

1. Table A1: Energy Circuit Symbols
2. Table A2: Differential Equations for the Simulation Model
3. Table A3: Documentation of Data Used for Initial Evaluation of Model Parameters with Calculations, Assumptions, and References
4. Table A4: Coefficient Values for Preliminary Simulations

TABLE A1 ENERGY CIRCUIT SYMBOLS
(Odum 1971, 1972)

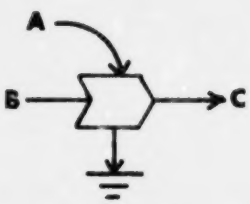
SYMBOL	FUNCTION
	External Driving Force
	Internal Energy Storage (state variable)
	Pathway of Energy Flow
	Heat Sink; Metabolic Energy Loss in Respiration
	Interactive Function of Two Factors (A and B) causing a Resultant Flow (C)
	Primary Producer
	Consumer

TABLE A2 DIFFERENTIAL EQUATIONS FOR THE STATE VARIABLES OF THE MODEL

NOTATION	DESCRIPTION
$X_i DOT$	= time rate of change of energy storage in compartment i
FX_iX_j	= energy flow from compartment i to compartment j
RX_i	= respiration of compartment i
FO_i	= primary production of compartment i
K_n	= exchange coefficient
X_i	= energy storage of compartment i
EX_i	= exchange of energy between compartment X_i and the sea
R	= Remixing Coefficient

Spartina

```
X1DOT=FO1-RX1-FX1X4-FX1X6-FX1X7-FX1X3-FX1X10
FO1=K1*SUN*TEMP*X1
RX1=K2*TEMP*X1**2
FX1X4=K3*TEMP*X1*X4
FX1X6=K4*X1
FX1X7=K5*X1
FX1X3=K6*X1
FX1X10=K7*X1
SUN=A+B*SIN(.0172*TIME)
TEMP=C+D*SIN(.0172*(TIME-40.))
SS=SUN*EXP(K8*AX1)
AX1=.6X1
```

(continued)

TABLE A2 (continued)

Particulate Organic Matter in the Water

```
      X9DOT=FO4+((A1/A2)*(FX3X9+FX2X9))+((A5/A2)*FX14X9)+(((A1+A5)...
/A2)*FX6X9)+((A3/A2)*(FX13X9+FX12X9))+FX10X9+FX11X9-FX9X6-FX9X11-...
FX9X12-FX9X17-FX9X10-RX9-EX9

FO4=K44*SUN*TEMP
FX13X9=K45*X130
FX12X9=K46*TEMP*(FX9X12+X10X12)*
FX10X9=K47*TEMP*X10*X9
FX11X9=K48*TEMP*X11
FX9X11=K49*TEMP*X9*X11
FX9X12=K50*TEMP*X9X120
FX9X17=K51*X9
FX9X10=K52*TEMP*X9
RX9=K53*TEMP*X9**2
R=.5+.4*SIN(.0172*TIME)
EX9=3.*KEXC9*(1.-R)*((X9/3.)-POMS)
```

Dissolved Organic Matter in the Water

```
      X10DOT=((A1/A2)*(FX7X10+FX1X10))+FX9X10+((A3/A2)*(X12X10+...
X13X10))+((A5/A2)*X14X10)*((A4/A2)*(X18X10+X15X10))+X11X10-FX10X9-...
X10X12-E10
*

X12X10=K54*TEMP*X120
X13X10=K55X130
X18X10=K56*X10
X15X10=K57*TEMP*X150
X11X10=K58*TEMP*X11
X10X12=K59*TEMP*X10*X120
E10=3.*KEX10*(1.-R)*((X10/3.)-DOMS)
```

Fish

```
      X11DOT=FX9X11+((A3/A2)*X12X11)+((A4/A2)*X15X11)-FX11X8-FX11X9-...
X11X10-RX11
*

X12X11=K60*TEMP*X120*X11
X15X11=K61*TEMP*X150*X11
RX11=K62*TEMP*X11**2
*
```

This term in the equation for compartment X9 should have been ((A2/A3)(FX9X12)+X10X12. The results of a corrected simulation indicated that this omission caused less than 5% error in the results.

(continued)

TABLE A2 (continued)

Marsh Macrofauna

```
X4DOT=FX1X4+FX2X4+FX5X4+FX6X4-FX4X8-FX4X6-RX4-FX4X7
FX5X4=K19*TEMP*X5*X4
FX6X4=K20*TEMP*X6*X4
FX4X8=K21*X4*X8
FX4X6=K22*X4
RX4=K23*TEMP*X4**2
FX4X7=K24*X4
```

Marsh Meiofauna

```
X5DOT=FX2X5+FX6X5-FX5X4-RX5-FX5X6-FX5X7
FX6X5=K25*TEMP*X6*X5
RX5=K26*TEMP*X5**2
FX5X6=K27*X5
FX5X7=K28*X5
```

Sediment Detritus and Bacteria (Marsh)

```
     X6DOT=FX1X6+FX2X6+FX3X6+FX4X6+FX5X6+FX8X6+((A2/A1)*FX9X6)+...
((A5/A1)*FX14X6-RX6-FX6X4-FX6X5-FX6X7-FX6X9
FX8X6=K29*X8
FX9X6=K30*X9
FX14X6=K31*X14
RX6=K32*TEMP*X6**2
FX6X7=K33*X6
FX6X9=K34*X6
```

Dissolved Organic Matter in Marsh Sediments

```
X7DOT=FX1X7+FX2X7+FX4X7+FX5X7+FX6X7-FX7X10
FX7X10=K35*X7
```

Birds

```
X8DOT=FX4X8+((A2/A1)*FX11X8)+((A3/A1)*FX12X8)-FX8X6-RX8
FX11X8=K36*X11*X8
FX12X8=K37*X120*X8
RX8=K38*X8**2
```

(continued)

TABLE A2 (continued)

Microbenthic Algae on Mud Flats

```
X14DOT=FO3-RX14-X14X15-X14X10-FX14X9-FX14X6
FO3=K39*SUN*TEMP*X14
RX14=K40*TEMP*X14**2
FX14X9=K42X14
X14X15=K41*TEMP*X14*X150
X14X10=K43*X14
```

Marsh Algae

```
X2DOT=FO2-RX2-FX2X4-FX2X5-FX2X6-FX2X9-FX2X7
FO2=K9*SS*TEMP*X2
RX2=K10*TEMP*X2**2
FX2X4=K11*TEMP*X2*X4
FX2X5=K12*TEMP*X2*X5
FX2X6=K13*X2
FX2X9=K14*X2
FX2X7=K15*X2
```

Above Ground Detritus and Bacteria

```
X3DOT=FX1X3-RX3-FX3X6-FX3X9
RX3=K16*TEMP*X3**2
FX3X6=K17*X3
FX3X9=K18*X3
```

TABLE A3 DOCUMENTATION OF DATA USED FOR INITIAL EVALUATION OF MODEI PARAMETERS WITH CALCULATIONS, ASSUMPTIONS, AND REFERENCES

Compartment or Flow	Value	Assumptions and Calculations	References
X1	1912.0	1. Spartina alterniflora (Tall) = 3.3 kcal/g dwt Spartina alterniflora (Short) = 2.6 kcal/g dwt	1. Nixon & Oviatt, 1973
		2. Assuming 5.0 kcal/g dwt organic matter (OM): S. alterniflora (Tall) = 0.66 gOM/gdwt S. alterniflora (Short) = 0.52 gOM/gdwt	
		3. Extant linear regressions for S. alterniflora (Tall) and S. alterniflora (Short): (Tall) y = 167.6 + 0.2x (y = g dwt; x = g wwt) (Short) y = 1.00 + 0.34	3. Reimold et al., 1975
		4. Tall S. alterniflora comprises 58% of Sapelo Island marsh and short S. alterniflora comprises 42%	4. Teal, 1962
		5. Standing crops for Sapelo Island marsh are: Tall S. alterniflora = 1987.5 gwwt/m^2 Short S. alterniflora = 660.0 gwwt/m^2	5. Teal, 1962
		6. Assuming #1 and #3 are applicable to Sapelo Island Spartina alterniflora: Short Spartina = .42 x .52 x 225.4 gdwt/m^2 = 49.23 gdwt OM/m^2 Tall Spartina = .58 x .66 x 564.7 gdwt/m^2 = 216.17 gdwt OM/m^2	

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
		(% marsh x organic matter conversion x standing crop of *Spartina* dry weight)	
		7. Conversion to kilocalories : (49.23 + 216.17) gdwt OM/m^2 x 5 kcal/gdwt OM = 1326.97 kcal/m^2 for above-ground biomass	
		8. *Spartina* roots comprise 58.5 gC/m^2 = 585 kcal/m^2	8. Wiegert et al., 1975
		9. Total standing crop/m^2 = 585.0 + 1326.97 = 1912.0 kcal/m^2	
		10. Above-ground biomass = 69.4% of total standing crop	
FO1	94.74	1. Gross Production *Spartina alterniflora* = Net Production + Respiration Net Production = 6580 kcal/m^2 yr Respiration = 28000 kcal/m^2 yr Gross Production = 34580 kcal/m^2 yr = 94.74 kcal/m^2 day	1. Teal, 1962 Smalley, 1959 Teal & Kanwisher, 1961
RX1	76.71	1. *Spartina alterniflora* respiration = 28000 kcal/m^2 yr = 76.71 kcal/m^2 day	1. Teal & Kanwisher, 1961
FX1X4	0.836	1. Herbivore grazing of *Spartina* = 305 kcal/m^2 yr = 0.836 kcal/m^2 day	1. Teal, 1962

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
FX1X6	5.83	1. Flow to sediment detritus from roots mortality = Flow into roots compartment - Flows out of roots compartment = Production of roots - Respiration of roots - Flow to *Spartina* leaves - Flow to sediment DOM = 43.3 kcal/m^2 day - 35.1 kcal/m^2 day - 1.2 kcal/m^2 day - 1.17 kcal/m^2 day = 5.83 kcal/m^2 day	1. Wiegert et al., 1975
FX1X7	1.17	1. Flow to sediment DOM = Daily transfer rate of 0.2% 2. .002 x Root Biomass (585 kcal/m^2) = 1.17 kcal/m^2 day	1. Wiegert et al., 1975
FX1X10	0.167	1. DOC release into water column by *Spartina* leaves = 125 µg DOC/gdwt hr 2. Dry weight = 422.194 gdwt/m^2 and leaves make up 45% of above ground biomass; applicable dry weight = 190.999 gdwt/m^2 3. 125 g DOC/gdwt hr x 190.999 gdwt/m^2 x .7 hr/day = .0167 µg DOC/m^2 day = .167 kcal/m^2 day	1. Gallagher et al., 1976 2. Pfeiffer et al., 1973 3. Gallagher et al., 1976
FX1X3	10.027	1. Inputs = Outputs (Steady State) 2. Mortality of *Spartina* = 10.027 kcal/m^2 day	
X2	75.92	1. Average of 15.184 µg Cl a/cm^2 of marsh surface	1. Pomeroy, 1959 Estrada et al. 1974

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
		2. 15.184 g Cl a/cm^2 = 0.15184 g Cl a/m^2 3. 0.15184 g Cl a/m^2 = 7.592 g C/m^2 4. 7.592 g C/m^2 = 75.92 kcal/m^2	3. Strickland, 1965
FO2	4.93	1. Gross production of algae = 1800 kcal/m^2 year = 4.93 kcal/m^2 day	1. Pomeroy, 1959
RX2	0.49	1. Respiration of marsh algae = Gross production minus net production = 1800 kcal/m^2 year - 1620 kcal/m^2 year = 180 kcal/m^2 year = 0.49 kcal/m^2 year	1. Pomeroy, 1959
FX2X4	0.312	1. Assume algal grazing by herbivores is 33% of remaining macro-consumer consumption = .333(342 kcal/m^2 year) = 0.312 kcal/m^2 day	1. Teal, 1962
FX2X5	0.1096	1. Assume 33% of meio-consumer consumption is algal grazing = .333(110 kcal/m^2 year) = .1096 kcal/m^2 day	1. Teal, 1962
FX2X6	3.306	1. Assume 90% of senescent mortality goes to sediment detritus = .90(3.6729 kcal/m^2 day) = 3.306 kcal/m^2 day	1. Teal, 1962 Pomeroy, 1959
FX2X9	0.367	1. Assume 10% of senescent mortality is washed away by the tides = .10(3.6729 kcal/m^2 day) = 0.367 kcal/m^2 day	1. Teal, 1962

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
FX2X7	0.3451	1. DOM loss to sediment DOM pool equals 7% of gross production .07(4.93 kcal/m^2 day) = 0.3451 kcal/m^2 day	1. Hellebust, 1965
X3	1180.0	1. Standing crop of dead Spartina = 118.0 g C/m^2 = 1180 kcal/m^2 2. Assumes bacterial biomass negligible	1. Wiegert et al., 1975
FX1X3	10.027	1. Mortality of Spartina alterniflora; See Compartment X1	
RX3	2.74	1. Respiration of bacteria in dead Spartina detritus = 1000 kcal/m^2 year = 2.74 kcal/m^2 day	1. Teal, 1962
FX3X6	0.72	1. Flow to soil detritus is 10% of detrital flow; calculated from input-output analysis detrital flow equals 7.203 .10(7.203 kcal/m^2 day) = .72 kcal/m^2 day	
FX3X9	6.483	1. Detrital flow to water column equals remaining detrital flow or 90% of total detrital flow = 6.483 kcal/m^2 day	
X4	19.77	1a. Insects: Respiratory Turnover Time = 1.4 days (RTT) 1b. Insect respiration rate = 224 kcal/m^2 year 1c. Insect standing crop =	1a. Day et al., 1973 1b. Teal, 1962

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
		$\frac{\text{(Respiratory Rate)(Respiratory TT)}}{\text{(\# days/year)(kcal/g dwt organic matter)}}$	
		$\frac{(224\ \text{kcal/m}^2\ \text{year})(1.4\ \text{days})}{(365\ \text{days})(5.0\ \text{kcal/g dwt OM})}$	
		$= 0.17\ \text{gOM/m}^2$	
		2a. Spiders; RTT = 1.4 days	2a. Day et al., 1973
		2b. Respiration rate = 23 kcal/m^2 year	2b. Teal, 1962
		2c. Standing crop = 0.0176 gOM/m^2	
		3a. Crabs (Uca spp. and Sesarma spp.) RTT = 20 days	3a. Day et al., 1973
		3b. Respiration rate = 170.6 kcal/m^2 year	3b. Teal, 1962
		3c. Standing crop = 1.87 gOM/m^2	
		4a. Mussels; RTT = 20 days (oysters)	4a. Day et al., 1973
		4b. Respiration rate = 39 kcal/m^2 year	4b. Teal, 1962
		4c. Standing crop = .24 gOM/m^2	
		5a. Mud crabs; RTT = 20 days	5a. Day et al., 1973
		5b. Respiration rate = 21.9 kcal/m^2 year	5b. Teal, 1962
		5c. Standing crop = 24 gOM/m^2	
		6a. Snails; RTT = 31.2 days	6a. Day et al., 1973
		6b. Respiration rate = 72 kcal/m^2 year	6b. Teal, 1962
		6c. Standing crop = 1.23 gOM/m^2	
		7. X4 = 5.0 kcal/g OM (0.17 + 0.0176 + 1.87 + .24 + .24 + 1.23) = 19.77 kcal/m^2	
FX2X4	0.312	1. See X2	

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
FX1X4	0.836	1. See X1	
FX6X4	0.56223	1. Assume two-thirds of algal-detrital flow to marsh macro-consumers is detritus of which 10% is meiofauna eaten in conjunction with detritus .6667(.9)(342 kcal/m^2 yr) = 0.56223 kcal/m^2 day	1. Teal, 1962
FX4X8	0.045	1. Input to birds via predation on macro-consumers = 7.33 gOM/m^2 yr 2. Assume 50% of this flow comes from fish and 50% from marsh community and oyster reefs 3. Assume 15% of marsh community flow comes from oyster reef community (i.e., 7.5% of total from oyster community) 4. Grazing on Macro-consumers by birds = .5 x (.85) x (36.65 kcal/m^2 yr) = 0.045 kcal/m^2 day	1. Day et al., 1973
FX4X6	.1724	1. Inputs = Outputs (Steady State) 2. Feeding via Spartina + Feeding via Algae + Feeding via Detritus + Feeding via Meiofauna - Predation by Birds - Respiration - DOM Excretion = FX4X6 = 0.1724 kcal/m^2 day	
RX4	1.508	1. Insect Respiration = 224 kcal/m^2 yr Spider Respiration = 23 kcal/m^2 yr Crab Respiration = 171 kcal/m^2 yr Mussel Respiration = 39 kcal/m^2 yr	1. Teal, 1962

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
		Snail Respiration = 72 kcal/m^2 yr Mud Crab Respiration = 21.9 kcal/m^2 yr	
		2. RX4 = 550.9 kcal/m^2 yr = 1.508 kcal/m^2 day	
FX5X4	0.6247	1. Ingestion of meiofauna with detritus is 10% of detrital-meiofaunal component = .6667(1)(342 kcal/m^2 yr) = .06247 kcal/m^2 day	
FX4X7	0.473	1. Excretion of DOM = .5 mg C/gdwt/hr	1. Johannes & Satomi, 1967
		2. FX4X7 = .5 mg C/gdwt/hr (3.954 gdwt)(24hr) = .0473 kcal/m^2 day	
X5	1.372	1. Nematodes = 2.76 gwwt/m^2 Assuming 10 gwwt = 1 gdwt Biomass = .276 gdwt/m^2	1. Teal, 1962
		2. Assuming 90% organic matter/gdwt Biomass = .2484 gOM/m^2 Biomass = 1.242 kcal/m^2	
		3. Annelids = Winter: 33.56 individuals/.01m^2 Summer: 23.64 individuals/.01m^2 Average weight = .1 mg wwt Average wwt Biomass Winter = 335.6 mg/m^2 Average wwt Biomass Summer = 236.4 mg/m^2	3. Teal, 1962
		4. Mean wwt Biomass = 286 mg/m^2 Biomass dwt = 28.6 mg dwt/m^2	
		5. Biomass = .026 gOM/m^2 Biomass = .130 kcal/m^2	

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
		6. X5 = (1.242 + .130) kcal/m^2 = 1.372 kcal/m^2	
FX5X4	.06247	1. See X4	
FX2X5	.1096	1. See X2	
FX6X5	.2203	1. Assume two-thirds of algal-detrital flow to meioconsumers is detritus	
		2. .667(110 kcal/m^2 yr) = .2203 kcal/m^2 day	2. Teal, 1962
RX5	.247	1. Meioconsumers respiration = 90 kcal/m^2 yr = .274 kcal/m^2 day	1. Teal, 1962
FX5X7	.014	1. Assume DOM excretion is 1% of standing crop/day = .014 kcal/m^2 day	
FX5X6	.00653	1. Input = Output (Steady State) Feeding via Algae + Feeding via Detritus - Respiration - Predation by Macro-consumers - DOM Excretion = FX5X6 = .00653 kcal/m^2 day	
X6	1.75E+5	1. Standing Crop Detritus in Sediments = 17.5E+3 g C/m^2	1. Wiegert et al., 1975
		2. Bacterial Biomass (54 kcal/m^2) is negligible	2. Wiegert et al., 1975
		3. X6 = 1.75E+5 kcal/m^2	
FX2X6	3.306	1. See X2	
FX1X6	5.83	1. See X1	
FX3X6	.72	1. See X3	

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
FX4X6	.1724	1. See X4	
FX5X6	.00653	1. See X5	
FX8X6	.0304	1. Feces and Mortality of birds = 2.222 gOM/m^2 yr = .0304 kcal/m^2 day	1. Day et al., 1973
FX6X7	0.54	1. Release of DOM to sediment pool is 1% of bacterial standing crop = .01(54 kcal/m^2) = .54 kcal/m^2 day	1. Wiegert et al., 1975
RX6	5.483	1. Respiration of marsh sediment = 2090 kcal/m^2 yr = 5.726 kcal/m^2 day	1. Teal & Kanwisher, 1961
		2. This includes meio-consumer respiration which equals 0.247 kcal/m^2 day	
		3. RX6 = 5.726 kcal/m^2 day - 0.247 kcal/m^2 day = 5.483 kcal/m^2 day	
FX14X6	10.283	1. Mortality to sediments from mudflat microalgae equals 10.283 kcal/m^2 day (See X14)	
		2. Prorated by area of mudflats (82E+6 m^2) and area or marsh (2513E+6 m^2) = 0.3355 kcal/m^2 day	
FX6X4	0.56223	1. Grazing of detritus by macro-consumers - see X4	
FX6X5	0.2203	1. Intake of detritus by meio-consumers - see X5	
FX9X6	1.155	1. Sedimentation over marsh by water column = 0.326 kcal/m^2 day	1. Wiegert et al., 1975

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
		2. Prorated by the area of the marsh (2513E+6 m^2) and the area of the water column (709E+6 m^2) = 1.155 kcal/m^2 day lost from water column	
FX6X9	3.25	1. Input = Output (Steady State)	
		2. Difference here = 3.25 kcal/m^2 day	
X7	20.0	1. DOM (Dissolved Organic Matter) in sediment pool = 4.0 g C/m^2 = 20.0 kcal/m^2	1. Wiegert et al., 1975
FX1X7	1.17	1. See X1	
FX2X7	.3451	1. See X2	
FX4X7	.0473	1. See X4	
FX5X7	.014	1. See X5	
FX6X7	0.54	1. See X6	
FX7X10	2.1164	1. Release of dissolved organic matter from sediment pool to water column	
		2. Input = Output (Steady State)	
		3. Difference equals 2.1164 kcal/m^2 day	
X8	0.22	1. Bird Biomass = 0.044 gOM/m^2 = 0.22 kcal/m^2	1. Day et al., 1973
FX8X6	0.0304	1. See X6	
FX4X8	0.045	1. See X4	

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
RX8	0.07	1. Bird Respiration = 5.11 gOM/m^2 yr = 0.07 kcal/m^2 day	1. Day et al., 1973
FX12X8	0.0947	1. Predation on oyster community by birds is assumed to be 7.5% of total ingestion (see X4)	
		2. Total Ingestion = 7.33 gOM/m^2 yr	2. Day et al., 1973
		3. Ingestion via oyster community = 0.005 kcal/m^2 day	
		4. Prorated over area of oyster communities (137E+6 m^2) and area of marsh (2513E+6 m^2) = .0947 kcal/m^2 day lost from oyster community	
X14	150.0	1. Biomass of benthic microalgae = 300 mg Cl a/m^2	1. Zingmark, Unpubl. Data
		2. 0.3 g Cl a/m^2 = 15.0 g C/m^2 = 150.0 kcal/m^2	
FO3	45.05	1. Net Production = 685 g C/m^2 yr = 1.8767 g C/m^2 day = 18.767 kcal/m^2 day	1. Zingmark, Unpubl. Data
		2. Assuming night respiration = 40% of light respiration and that light respiration = Net Productivity; Total Respiration = 1.4 x Net Production = 26.274 kcal/m^2 day	
		3. Gross Production = Net Production + Respiration = 45.05 kcal/m^2 day	
RX14	26.274	1. See above; FO3	
FX14X15	1.915	1. Assume macrobenthic consumer intake of microbenthic algae is 18.75% of total intake (i.e., algal and	

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
		macrophyte ingestion by benthic macro-consumers represents 25% of total intake and algal ingestion represents 75% of that flow or 18.75%) 2. Total Macro-consumer intake = 1.074 kcal/m^2 day (see X15) 3. .1875(1.074 kcal/m^2 day) = 0.2014 kcal/m^2 day 4. Prorated by area of benthos (799.9E+6 m^2) and area of mudflat (82E+6 m^2) = 1.915 kcal/m^2 day	
FX14X10	3.15	1. DOM loss equals 7% of gross production	1. Hellebust, 1965
FX14X9	3.42774	1. Input = Output (Steady State) 2. Total Mortality of microalgal compartment = 13.711 kcal/m^2 day 3. Assuming 25% of this is washed out by tides FX14X9 = 3.42775 kcal/m^2 day	
FX14X6	10.28325	1. Total detrital flow from microalgal compartment = 13.711 kcal/m^2 day 2. Assuming 75% is trapped in sediment and thus returns to sediment; FX14X6 = .75(13.711 kcal/m^2 day = 10.28325 kcal/m^2 day 3. Prorated by area of mudflats (82E+6 m^2) and area of marsh (2513E+6)(as sediment detritus computed only for marsh and not mudflat; marsh area becomes 2595E+6 m^2 and gain to sediment = 0.3355 kcal/m^2 day	

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
X9	58.8	1. Water column particulate matter composed of phytoplankton, detritus, attendant microbes, and zooplankton	
		2. Phytoplankton = 4.02 mg Cl a/m^3	2. Erkenbrecher, 1976
		Assuming average depth of 3 meters, = 12.06 mg Cl a/m^2	
		Assuming 50 mg C/mg Cl a, = 603 mg C/m^2	Strickland, 1965
		= 0.603 g C/m^2 = 6.03 kcal/m^2	
		3. Zooplankton = 0.024 g C/m^2 = 0.24 kcal/m^2	3. Coull, 1977
		4. Total water column ATP = 1.31 mg/m^3	4. Erkenbrecher, 1976
		Assuming 250 mg C/mg ATP and average depth of 3 meters,	Holm-Hansen & Paerl, 1972
		= 982.5 mg C/m^2	
		Subtracting from this value the value of phytoplankton and zooplankton;	
		0.9825 g C/m^2 - 0.603 g C/m^2 - 0.024 g C/m^2 = 0.3555 g C/m^2 (microbial biomass) = 3.555 kcal/m^2	
		5. Detrital POC (particulate organic carbon) = Total POC - Total ATP carbon	

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
		Total POC = 1.96 g C/m^3 5.88 g C/m^2 Subtracting out living carbon; 5.88 g C/m^2 - 0.9825 g C/m^2 = 4.8975 g C/m^2 = detrital POC = 48.975 kcal/m^2	5. Erkenbrecher, 1976
		6. Total particulate organic matter in water column = Phytoplankton + Zooplankton + Microbial Biomass + Detrital Value 6.03 kcal/m^2 + 0.24 kcal/m^2 + 3.555 kcal/m^2 + 48.975 kcal/m^2 = 58.8 kcal/m^2	
FO4	15.0	1. Net productivity of estuarine phytoplankton = 273 g C/m^2 yr = 0.75 g C/m^2 day 2. Assuming total respiration (light and dark each) equals net production; FO4 = 2(.75 g C/m^2 day) = 1.5 g C/m^2 day = 15.0 kcal/m^2 day	1. Zingmark, 1977
FX3X9	6.483	1. See X3 2. Prorated by the spatial areas of the water column and the marsh surfaces; FX3X9 = incoming flow of 22.979 kcal/m^2 day	Table 1
FX2X9	0.367	1. See X2 2. Prorated as above; FX2X9 = incoming flow of 1.3 kcal/m^2 day	

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
FX14X9	3.42775	1. See X14	Table 1
		2. Prorated according to the areas of the water and mudflats	
FX6X9	3.25	1. See X6	
		2. Prorated by areas of marsh + mudflats and water column;	
		FX6X9 = incoming flow of 11.89 kcal/m^2 day	
FX13X9	6.8148	1. Senescent mortality of macrobenthic algae (see X13) = 6.8148 kcal/m^2 day (by input-output difference analysis)	
		2. Prorated by areas of oyster reefs and water column	Table 1
		FX13X9 = incoming flow of 1.317 kcal/m^2 day	
FX12X9	27.66	1. Throughflow of filter-feeding organisms in oyster reef community = 27.66 kcal/m^2 day (see X12)	1. Dame & Stevens, 1977
		2. Prorated by areas of oyster reefs and water column;	
		FX12X9 = incoming flow of 5.345 kcal/m^2 day	
FX10X9	3.266	1. Average concentration of dissolved organic matter in water column = 17.7 g C/m^2 = 5.9 g C/m^3 = 5.9 mg C/l = 5.9 x 10^3 ug C/l	1. Erkenbrecher, 1976

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
		2. Assuming all amino acids are equally distributed;	2. Crawford et. al., 1974
		V(max) = 2.4143 ug C/l hr K = 17.846 ug C/l	
		3. Using Michaelis-Menten equation:	
		$v = \frac{V(max) \times Concentration}{K + Concentration}$	
		$v = \frac{2.4143 \text{ ug C/l hr} \times 5.9 \times 10^3 \text{ ug C/l}}{17.846 \text{ ug C/l} \times 5.9 \times 10^3 \text{ ug C/l}}$	
		$v = 2.407 \text{ mg C/m}^3 \text{ hr}$	
		$v = 1.733 \text{ kcal/m}^2 \text{ day}$	
		4. Glucose uptake = V(max) = 2.13 ug C/l hr K = 4.00 ug C/l	
		$v = 2.1286 \text{ mg C/m}^3 \text{ hr} = 1.5326 \text{ kcal/m}^2 \text{ day}$	4. Crawford et. al., 1974
		5. FX10X9 = 1.733 kcal/m^2 day + 1.5526 kcal/m^2 day = 3.2656 kcal/m^2 day	
FX11X9	.273	1. Feces loss from fish equals 22.735 g OM/g OM of fish yr	1. Day et. al., 1973
		2. Standing Crop of Fish biomass = 0.876 g OM/m^2 (see X11))	2. Moore, Unpubl. Data
		3. FX11X9 = (22.735 g OM/g OM fish yr) x (0.876 g OM/m^2) = 19.916 g OM/m^2 yr = 0.273 kcal/m^2 day	

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TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
FX9X6	1.155	1. Sedimentation rate (see X6)	1. Wiegert et. al., 1975
FX9X11	0.551	1. See X11	
FX9X12	9.066	1. Filtration rate of oyster reef consumers = 46.9205 kcal/m^2 day (see X12)	1. Dame & Stevens, 1977
		2. Prorated by areas of oyster reef and water column; FX9X12 = loss from water column of 9.066 kcal/m^2 day	
FX9X17	4.62	1. See X17; found by input-output difference analysis = 4.62 kcal/m^2 day loss from water column	
FX9X10	1.21	1. Phytoplankton excretion = 7% (average) of photoassimilated carbon	1. Hellebust, 1965
		2. Gross Production of phytoplankton = 15.0 kcal/m^2 day = 1.5 g C/m^2 day	2. Zingmark, 1977
		3. .07(1.5 g C/m^2 day) = 1.05 kcal/m^2 day	
		4. Zooplankton excretion = (1.0 x T) - 5.9 = mg a-amino N/g Dwt-day	4. Johannes & Webb, 1965
		5. Mean temperature = 17.5 C	5. National Weather Service
		6. (1.0 x 17.5) - 5.9 = 11.6 mg a-amino N/g dwt-day	
		7. Standing biomass of zooplankton = 48 mg dwt/m^2	6. Coull, 1977

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TABLE A3 (continued)

Compartment or Flow	Value	Assumption and Calculations	References
		8. 4 x a-amino N = Organic carbon	7. Johannes & Webb, 1965
		9. 11.6 mg a-amino N/g dwt-day = 46.4 mg Org C/g dwt-day	
		10. 46.4 mg Org C/g dwt-day x 48 mg dwt/m^2 = 2.227 mg Org C/m^2-day	
		11. Zooplankton excretion = 0.0225 kcal/m^2-day	
		12. Substituting dwt of bacteria (microbes) in above equation; Bacterial excretion = 0.139 kcal/m^2-day	12. Bonnell, 1977
		13. Total excretion of DOM by living particulate matter = (1.05 + 0.0225 + 0.139) kcal/m^2-day = 1.21 kcal/m^2-day	
EX9 (Export of POM to coastal waters)	17.48	1. Assuming complete mixing on every tide and a constant tidal prism of 40% of low water estuarine volume;	1. Kjerfve, Pers. Comm.
		2. Assuming that tidal remixing (the return of water from the immediately preceding ebb flow) is maximal in spring and summer (90%) and minimal in fall and winter (10%) and is sinusoidal; i.e., R = .5 + .4sin(.0172 x TIME);	2. Kjerfve, Pers. Comm.
		3. The concentration in an embayment after a full tidal cycle can be described as: $C(p) = \frac{(Ve \times Ce) + ((1-R) \times VT \times Co) + (R \times VT \times Ce)}{Ve + VT}$	

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumption and Calculations	References

where:

Cp = Concentration of x in tidal plume
Ve = Water volume in estuary at low water
Ce = Concentration in estuarine waters at low water
R = Remixing coefficient
VT = Tidal volume (Prism volume)
Co = Concentration of x in coastal waters

4. Net exchange can be characterized as the difference between Ce and Cp if total mixing occurs

5. Net C(exchange) = Ce - Cp

6. As tidal prism is constant; VT = .4Ve

7. Substituting .4Ve for VT in Equation 3 gives:

$$Cp = \frac{(Ve \times Ce) + ((1-R) \times .4Ve \times Co) + (R \times .4Ve \times Ce)}{Ve + .4Ve}$$

8. Factoring out Ve gives:

$$Cp = \frac{Ce + ((1-R) \times .4Co) + (R \times .4Ce)}{1.4}$$

9. Net C(exchange = $Ce - \frac{(Ce + ((1-R) \times .4Co) + (R \times .4Ce))}{1.4}$

10. Net C(exchange) can also be expressed equal to some constant coefficient of exchange related to the difference in estuarine and coastal water concentration;

Net C(exchange) = K(exc) x ((Ce - (((1-R) x Co) + (R x Ce)))

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumption and Calculations	References
		11. Settling these two equations for net exchange equal to each other allows a solution for K(exc): K(exc) = 0.286/tide or 0.5714/day	
		12. Particulate organic matter concentration in estuary = 58.8 kcal/m^2 or 19.6 kcal/m^3	12. Erkenbrecher, 1976
		13. Particulate organic matter concentration in coastal water (Co) = 2.14 kcal/m^3	13. Stevenson, Upubl. Data
		14. EX9 = 17.48 kcal/m^2 day	
RX9	28.17	1. By input-output analysis of difference respiration of POM = 28.17 kcal/m^2-day	
X10	177.0	1. Dissolved organic matter in water column = 5.9 g C/m^3	1. Erkenbrecher, 1976
		2. Assuming average depth of 3 meters; = 17.7 g C/m^2 = 177 kcal/m^2	
FX7X10	2.116	1. See X7	
		2. Prorated by areas of marsh and water column = Inflow of 7.501 kcal/m^2-day	Table 1
FX9X10	1.21	1. See X9	
F::1X10	.167	1. See X1	
		2. Prorated by area of marsh and water column; = Inflow of 0.592 kcal/m^2-day	

(continued)

TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
FX12X10	0.100	1. Release of DOM by oysters = 0.100 kcal/m^2-day	
		2. DOM release from mollusc = .505 mg a-amino N/100 g dwt-day	2. Spitzer, 1937
		3. 1 mg a-amino N = 4 mg Org C	3. Johannes & Webb, 1965
		4. Biomass of oyster community = 503.2 g dwt/m^2	4. Dame & Stevens, 1977
		5. DOM release = 20.32 mg DOM/m^2-day = 0.1 kcal/m^2-day	
		6. Prorated by areas of oyster reef and water column; = Inflow of 0.019 kcal/m^2-day	
X13X10	1.4532	1. Assuming benthic macrophytes lose an equivalent amount of photoassimilated carbon (7%) as do microbenthic algae; DOM loss = 1.4532 kcal/m^2-day (see X13)	
		2. Prorated by areas of oyster reef and water column, = Inflow of 0.281 kcal/m^2-day	
X14X10	3.15	1. See X14	
		2. Prorated by areas of mudflats and water column, = Inflow of 0.364 kcal/m^2-day	
X18X10	.0241	1. By input-output differences analysis, loss from DOM sediment pool in benthos = 0.0241 kcal/m^2-day (see X18)	
		2. Prorated by areas of benthos and water column, = Inflow of 0.0265 kcal/m^2-day	

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TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
X15X10	0.348	1. DOM loss by benthic macroconsumers = 0.348 kcal/m^2-day (see X15)	1. Johannes & Satomi, 1967
		2. Prorated by areas of benthos and water column, = Inflow of 0.383 kcal/m^2-day	
X11X10	0.0438	1. DOM loss from fish = 0.0438 (see X11)	
FX10X9	3.266	1. See X9	
X10X12	.0002	1. oyster uptake of DOM = 15 ng DOC/hr-g wwt at 50 µg DOC/ml	1. Swift et. al., 1975
		2. DOM concentration in water column = 5.9 µg/ml	
		3. Experimental concentration = 50 µg DOC/ml = 100 µg DOM/ml	
		4. Ratio of Concentrations = 0.059	
		5. Experimental uptake = 15 ng DOC/hr g wwt = 30 ng DOM/hr g wwt	
		6. Applying ratio of 0.059 to uptake gives uptake of 1.77 ng DOM/hr g wwt	
		7. 1.77 ng DOM/hr-g wwt = 17.7 ng DOM/hr g dwt	
		8. Oyster reef predominately oyster biomass = 503.2 gdwt/m^2	1. Dame & Stevens, 1977
		9. Uptake by oysters = 0.000107 g DOM/m^2-day = .0005 kcal/m^2-day	

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TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
		10. Prorated by areas of oyster reef and water column, = Outflow of 0.0002 kcal/m^2-day from water column	
EX10	7.1395	1. Input-output difference analysis calculates export to be 7.1395 kcal/m^2-day at steady state	
		2. Calculation of KEX10 (coefficient of exchange) (for method see X9-ex9);	
		3. KEXC10+ = 8.4523E-2	
X11	4.38	1. Range of wet weights for fish in major channels of North Inlet: 1 g wwt - 6 g wwt	1. Moore, Pers. Comm.
		2. 0.25 g wwt = dwt (i.e., dwt = 25% wwt)	2. Moore, Pers. Comm.
		3. Biomass = 0.25 (3.5 g wwt/m^2) = 0.875 g dwt/m^2 = 4.38 kcal/m^2	
FX9X11	0.0551	1. Input-output analysis shows planktivore and detritivore intake = 0.0551 kcal/m^2-day	
X12X11	.2417	1. Fish feeding habits can be apportioned as: Herbivores and primary carnivores: 8.6% of intake; Mid-carnivores: 48.6% of intake; Carnivores: 43% of intake	1. Day et. al., 1973
		2. Assuming 15% of mid-carnivore intake is from oyster reef	
		3. Mid-carnivores consume 48.6% of fish intake which is 0.747 kcal/m^2-day-gdwt	3. Day et. al., 1973

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TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
		4. X12X11 = .15(.486)(.747 kcal/m^2-day-gdwt) (.876 gdwt/m^2) = 0.0467 kcal/m^2-day	
		5. Prorated by areas of oyster reef and water column, = Outflow from oyster consumers of 0.2417 kcal/m^2-day	
X15X11	.4911	1. Assuming remaining 85% of mid-carnivore diet and 50% of top carnivore diet is from macrobenthos (remaining 50% of top carnivore diet internal)	
		2. Mid-carnivore diet = .2647 kcal/m^2-day Top carnivore diet = 0.2755 kcal/m^2-day	
		3. Input to fish equals 0.5402 kcal/m^2-day	
		4. Prorated by area of subtidal benthos and water column, = Outflow from Macrobenthos of 0.4911 kcal/m^2-day	
FX11X8	.177	1. See X8	
		2. Prorated by area of marsh and water column, = Inflow to Birds of 0.05 kcal/m^2-day	
X11X10	.0438	1. DOM loss in fish equals 1% of standing crop	1. Wiegart et. al., 1975
		2. .01(4.83) = .0483 kcal/m^2-day	
FX11X9	0.273	1. Feces loss from fish equals 22.735 g OM/m^2 yr	1. Day et. al., 1973
		2. Standing crop of fish = 0.876 g OM/m^2	
		3. FX11X9 = (22.735 g OM/m^2-yr-gOM fish) x	

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TABLE A3 (continued)

Compartment or Flow	Value	Assumptions and Calculations	References
RX11	.147	1. Fish respiration = 7 cal/g dwt-hr 2. Standing stock = 0.876 g dwt/m^2 3. RX11 = 147 cal/m^2-day = .147 kcal/m^2-day	1. Nixon & Oviatt, 1973
X12	2516.	1. Average caloric value of oyster community at North Inlet = 2516. kcal/m^2	1. Dame & Stevens, 1977

TABLE A4 COEFFICIENT VALUES FOR PRELIMINARY SIMULATIONS*

K1 = 6.1470E-7	K35 = 1.0582E-1
K2 = 1.0651E-6	K36 = 1.8369E-1
K3 = 1.1227E-6	K37 = 1.7109E-4
K4 = 3.0492E-3	K38 = 1.44628
K5 = 6.1192E-4	K39 = 4.3503E-6
K6 = 5.2442E-3	K40 = 6.6728E-5
K7 = 8.7343E-5	K41 = 5.0312E-5
K8 = -2.6623E-3	K42 = 2 2852E-2
K9 = 1.2123E-5	K43 = 2.1E-2
K10 = 4.3154E-6	K44 = 2.1727E-4
K11 = 1.05518E-5	K45 = 4.7992E-2
K12 = 5.3412E-5	K46 = 3.3688E-2
K13 = 4.3546E-2	K47 = 1.7930E-5
K14 = 4.8340E-3	K48 = 3.5616E-3
K15 = 4.5456E-3	K49 = 1.2225E-5
K16 = 9.939E-8	K50 = 3.5018E-6
K17 = 6.1017E-4	K51 = 7.8571E-2
K18 = 5.4941E-3	K52 = 1.1759E-3
K19 = 1.1691E-4	K53 = 5.6229E-4
K20 = 8.2490E-9	K54 = 4.3152E-7
K21 = 1.0346E-2	K55 = 1.0234E-2
K22 = 8.7203E-3	K56 = 1.205E-3
K23 = 1.9585E-4	K57 = 1.3714E-3
K24 = 2.3925E-3	K58 = 5.7143E-4
K25 = 4.6575E-8	K59 = 2.5663E-11
K26 = 6.6607E-3	K60 = 1.2533E-6
K27 = 4.7595E-3	K61 = 4.4187E-4
K28 = 1.0204E-2	K62 = 4.3786E-4
K29 = 1.3818E-1	KEX09 = 0.4444
K30 = 1.9643E-2	KEX10 = 9.8748E-2
K31 = 6.8553E-2	A = 3945
K32 = 9.08802E-12	B = 1695
K33 = 3.0857E-6	C = 17.5
K34 = 1.8571E-5	D = 12.5

*1E-x is equivalent to 1 x 10^{-x}

SECTION 6

DEVELOPMENT OF A SALT MARSH MICROECOSYSTEM[1]

W. Kitchens

INTRODUCTION

In order for governmental agencies to anticipate and respond to problems arising from the ever-increasing encroachment of man on the invaluable, yet vulnerable, coastal wetlands (Gosselink et al., 1973; Odum and Odum, 1972; Odum, 1973; Vernberg, 1976), two approaches have evolved for generating predictive information for management strategies. Both approaches involve defining structural and functional components of the systems in question. The first approach is the development of ecosystem mathematical simulation models. To this end, several models of varying complexities have been generated for New England salt marshes (Nixon and Oviatt, 1973), the Gulf of Mexico salt marshes of the Mississippi River Delta (Day et al., 1973), and the Southeastern estuarine-salt marsh complexes (Vernberg et al., 1977; Weigert et al., 1975). These models are attempts to synthesize existing knowledge into a systematic and integrative scheme that developers hope will enable the modeler to make assessments at a holistic level regarding ecosystem responses to selected perturbations. Although these models are valuable in interpreting the interactive components of the ecosystem, as well as pinpointing "sensitive" areas or control mechanisms (Weigert et al., 1975), they simply do not have the resolution required for simulation and prediction of very specific environmental perturbations. Mann (in press) has drawn attention to the limitations of these and other similar models in application to these problems. He has suggested that one particular problem area is the lack of realistic validation procedures for ecosystem models.

The second approach is the "living" model or microecosystem approach. This approach also incorporates a holistic strategy to assess ecosystem structural and functional properties as well as responses to perturbations. Basically, this techniques involves "capturing" a viable part of the ecosystem in question and subjecting it to environmental regimes that simulate, as closely as possible, those of the natural system while at the same time maintaining some boundary control over these regimes for manipulative purposes. Ideally, these systems should be large enough to incorporate as many of the ecosystem components as possible without sacrificing ease of

[1]This section is in press in The International Journal of Environmental Studies.

replication, manipulation, and response measurements (Cooke, 1971). In the past, this approach has been successfully employed to investigate aspects of such fundamental ecosystem processes as nutrient cycling in aquatic systems (Whittaker, 1961), patterns of community metabolism (Beyers, 1963, 1965), patterns of ecological succession under various environmental regimes and stress (Cooke, 1967; Wilhm and Long, 1969), response to low fresh water flow regimes in estuaries (Cooper, 1970), and assorted community responses to environmental alterations in flowing streams (Kevern and Ball, 1965; Lauff and Cummings, 1964; McIntire et al., 1964; McIntire and Phinney, 1965; Odum and Hoskin, 1958). In addition, these "living" models can be excellent tools for the verification of mathematical models.

The purpose of this section is to present our design for a Spartina alterniflora salt marsh microecosystem and includes a rationale for, and data from, measurements detailing community structure and selected functional processes within the microecosystems.

The following criteria were incorporated within the design of the microecosystems: 1) the units would have to be replicable for use as a bioassay tool; 2) the units would have to be practical enough to be installed at various laboratory locations along the coast to assess local pollution problems; 3) the holistic response measurements would have to incorporate as much automation as feasible; 4) the construction and maintenance costs would have to be kept at a minimum; and 5) the results of tests within the units would have to be extrapolative to the natural ecosystem (community verification would be required).

METHODOLOGICAL APPROACH

Rationale

Figure 8 represents a very simplistic conceptual model of the community structure and energy flow pathways within the microecosystems. Inputs to the microecosystems are indicated on the left while exports are indicated to the right, except for Nitrogen. Since these systems are semi-enclosed by tank walls, the net resultant or culmination of all the pathways is the difference between inputs and exports. Since Copeland (1967) defines an environmental stress as any factor that alters these normal pathways, we have speculated that for these "living" models the best index of any stress (whether directly applied or by natural means) is reflected as a discrepancy between the input-output characteristics before and after any perturbations. Hence, we have designed the seawater system in such a manner as to be able to budget the fluxes of water and its constituents in and out of the systems on any time scale (see following sections). We have initiated some preliminary tidal budget studies for the fluxes of selected nutrients (see following sections).

In addition to the nutrient flux studies, we have also designed the systems for primary productivity studies for the following reasons: 1) they have been shown to be a sensitive index of community imbalances in various aquatic systems (Copeland, 1965, 1967; Copeland and Dorris, 1964); 2) replicated laboratory aquatic systems do not differ significantly with respect

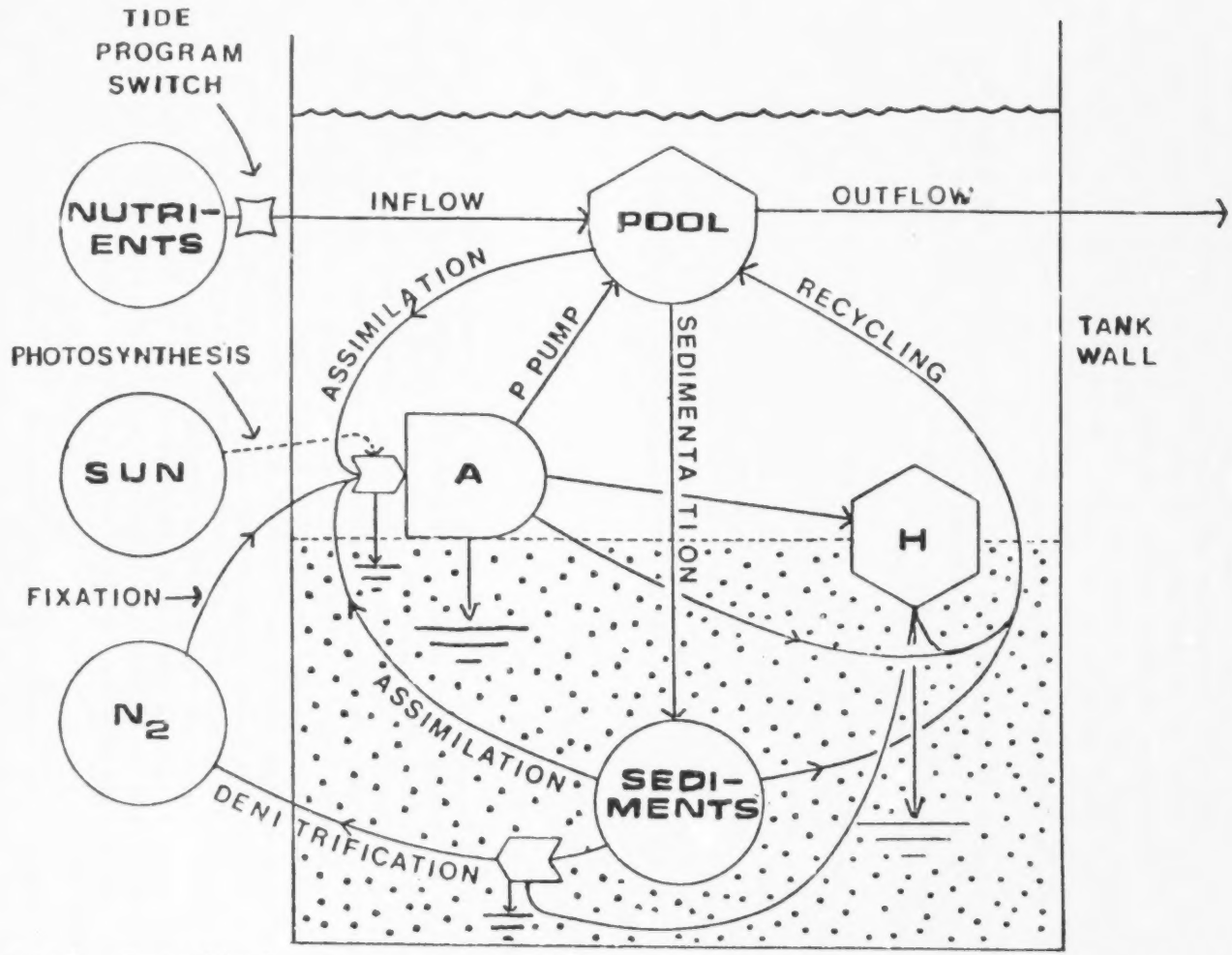

Figure 8. Generalized conceptual model depicting nutrient flow pathways in the microecosystem.

to levels of community metabolism (Abbot, 1966) ; and 3) the ease of automation for the measurement of the response.

In addition to these holistic response determinations, we have selected to monitor the macro- and meiobenthic faunal communities for the following reasons: 1) since these organisms are relatively sessile, they are directly subject to any environmental stress applied to the systems; 2) the communities have sufficient regeneration times which would facilitate monitoring subtle stress responses or recovery of the systems; and 3) these surveys allow one to compare the microecosystems directly with the natural systems.

Design and Preliminary Results

Design--

The microecosystems consist of four square tanks, each containing approximately six square meters of short Spartina alterniflora marsh. The units function as both holding tanks and metabolism chambers for productivity measurements. All associated support and monitoring systems are automated to operate with a minimum of supervision.

The size of the marsh plots minimizes edge effects found in smaller units without sacrificing sampling convenience and experimental control. Marsh was transplanted from the high marsh zone in the form of square sod blocks incorporating approximately 1000 cm^2 of the marsh with substrate intact to a depth of 20 cm. Observations during transplanting showed that this was deep enough to include the majority of the root mass and virtually all of the attendant faunal community. Sod blocks were reassambled in the tanks by using a random numbering arrangement. Initial attempts at establishing a viable marsh with the sod resting directly on the tank bottoms failed due to water pooling which damaged the root stock. A bottom layer of pea gravel was added to improve drainage and prevent pooling. This type of drainage design simulates interstitial drainage as observed at the control site. A cross section of a tank unit is illustrated in Figure 9.

The microecosystems were maintained with a flow-through seawater system designed to simulate natural tidal regimes. A semi-diurnal tide, coincident with the natural tide, is provided by initiating a flooding of the tanks at 12-hour and 20-minute intervals. Duration and depth of inundation represent average annual conditions at the control site. With minor variations, daily tides 10 cm in depth inundate the substrate for two and one-half hours per cycle. Water movement across the substrate simulates sheet flow. This flow-through design maintains high water quality. The observed presence of viable meroplankton insures natural recruitment of benthic organisms.

A diagram of the seawater system is shown in Figure 10. Water is pumped continuously form the source creek adjacent to the control marsh to a 3000 liter head tank. Water flows into the bottom of the tank and overflows through an outlet at the top into a holding pond. Residence time within the head tank is approximately 15 minutes. To create a flood tide, water is diverted from the head tank through a solenoid valve and into a branching supply network to the tank inputs. After passing over the marsh surface, water flows out through baffled drains into the holding pond. In line

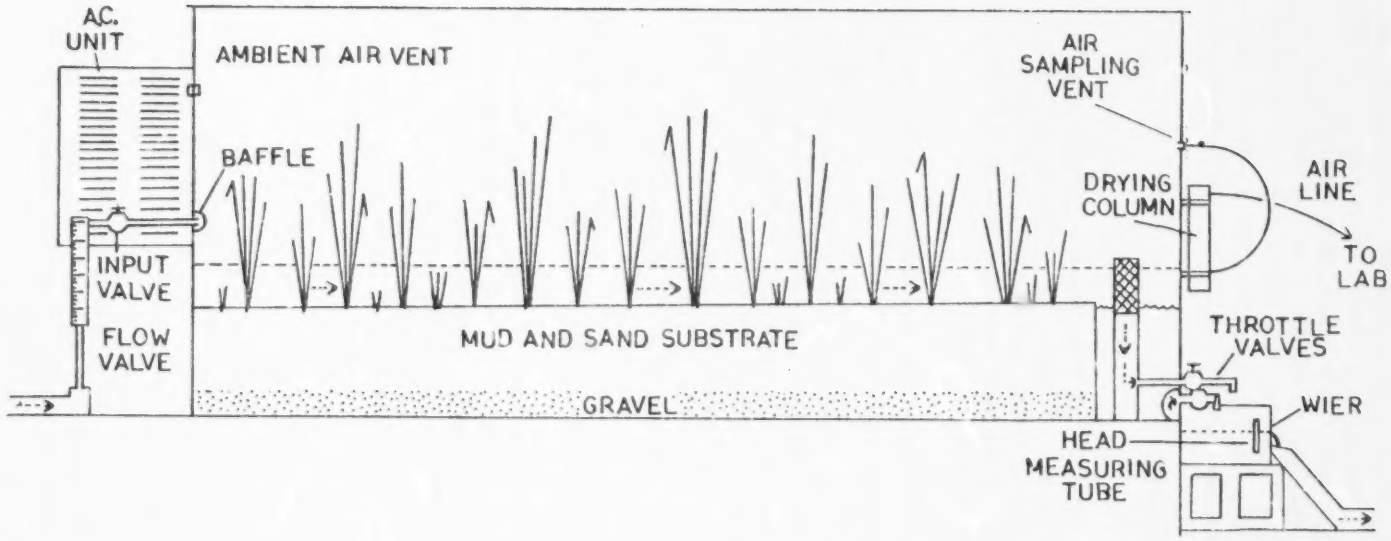

Figure 9. Cross section of a tank microecosystem unit

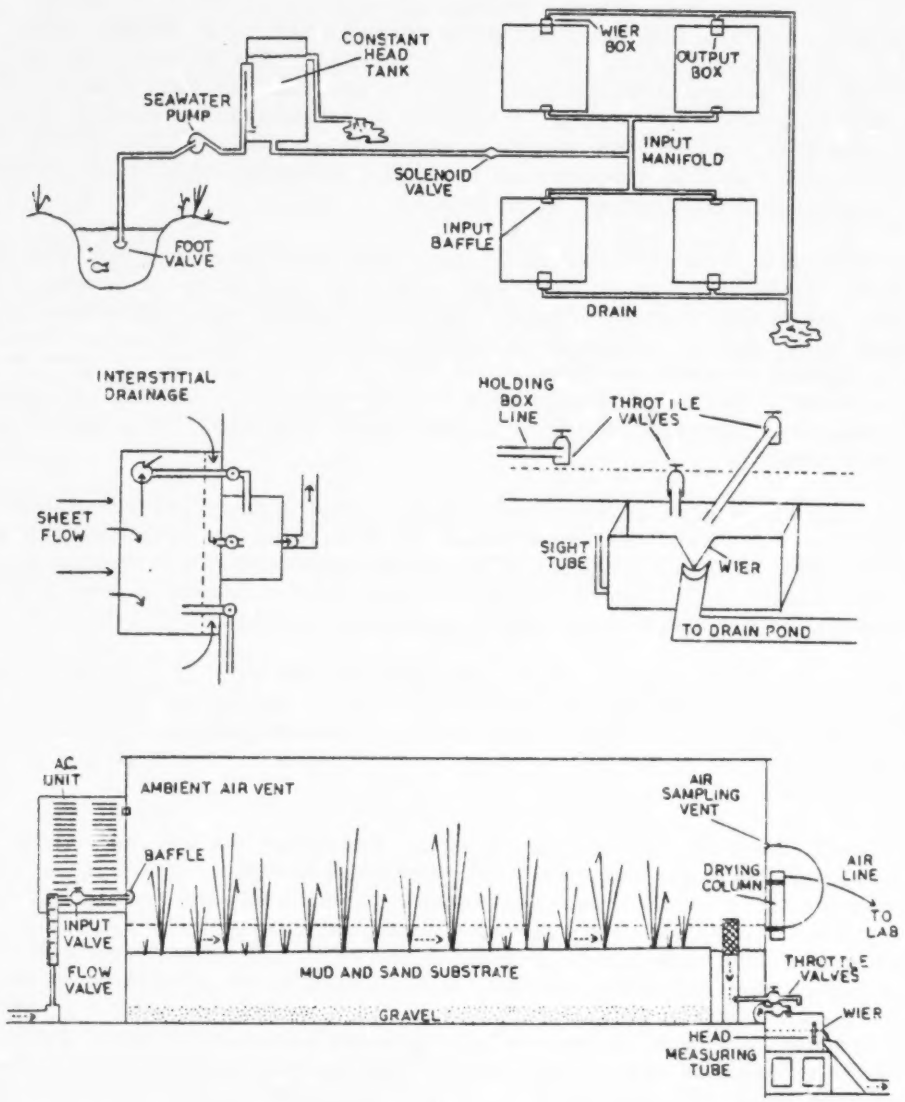

Figure 10. Schematic of seawater system.

flowmeters on the input side and calibrated wiers on the output side provide accurate measurements of water flow.

The air sampling system for the productivity measurements is also a flow-through design. During productivity measurements, air trapped in the chambers is continuously pumped through polyethylene tubing into the laboratory, where the CO_2 concentration is recorded by a Beckman 865 Infrared Gas Analyzer (IRGA) at hourly intervals. Air removed for analysis is replaced by ambient air through vents in the tank walls. Ambient CO_2 levels are also measured hourly to correct for atmospheric carbon drawn in through the wall vents. The constant addition of ambient CO_2 prevents the depletion of CO_2 in the chamber due to high photosynthetic rates. The air sampling system is diagrammed in Figure 11.

Diaphragm air pumps situated in the laboratory draw air out the sampling vents, through drying columns and into the laboratory at a rate of $0.3m^3$ per hour. Air is then pumped into a switching manifold where it can be routed to either an infrared gas analyzer or an exhaust vent. Each of the five sample streams is diverted through the analyzer for a period of twelve minutes. Halfway through each sampling period, the CO_2 concentration of the sample is recorded along with the date, time, and air temperature within the tank.

To trap air during productivity runs, translucent lids are bolted to the chambers. The lids are constructed of fiberglass greenhouse panels, with a transmittance of 95% in the visible light range. Since the lids are in place only during productivity measurements, the microecosystems are subjected to normal ambient weather conditions at all other times.

Window type air conditioners installed in the tank walls compensate for heat buildup due to the greenhouse effect. Cooling is controlled by a differential temperature controller situated on one of the tank walls. Measured variations from tank to tank do not exceed 1^oC and from tank to ambient are within $+2^oC$.

To test how well the microecosystems simulated the natural marsh community, two separate benthic surveys were conducted. The first, a nine-month macrobenthic survey, was initiated in June 1976 and terminated in February 1977. Samples were taken and analyzed quarterly. Four core samples were taken from the microecosystems (one sample/microecosystem). These samples were selected randomly within each microecosystem by using a grid and random number technique. In addition, eight random core samples were extracted from the control site. Four of these cores were analyzed and four were used as replacement cores for the microecosystem replicates. Core samples were extracted with a 10 x 20 centimeter P.V.C. manual cylindrical coring device and were seived (one millimeter mesh). Numbers of species and individuals were normalized to meter square values.

The other benthic survey was a meiobenthic survey initiated in July 1976 and terminated in May 1977. Samples for these surveys were made on a monthly basis. By using a grid and random-number technique, twelve core samples were randomly selected from the microecosystems (three samples/mi-

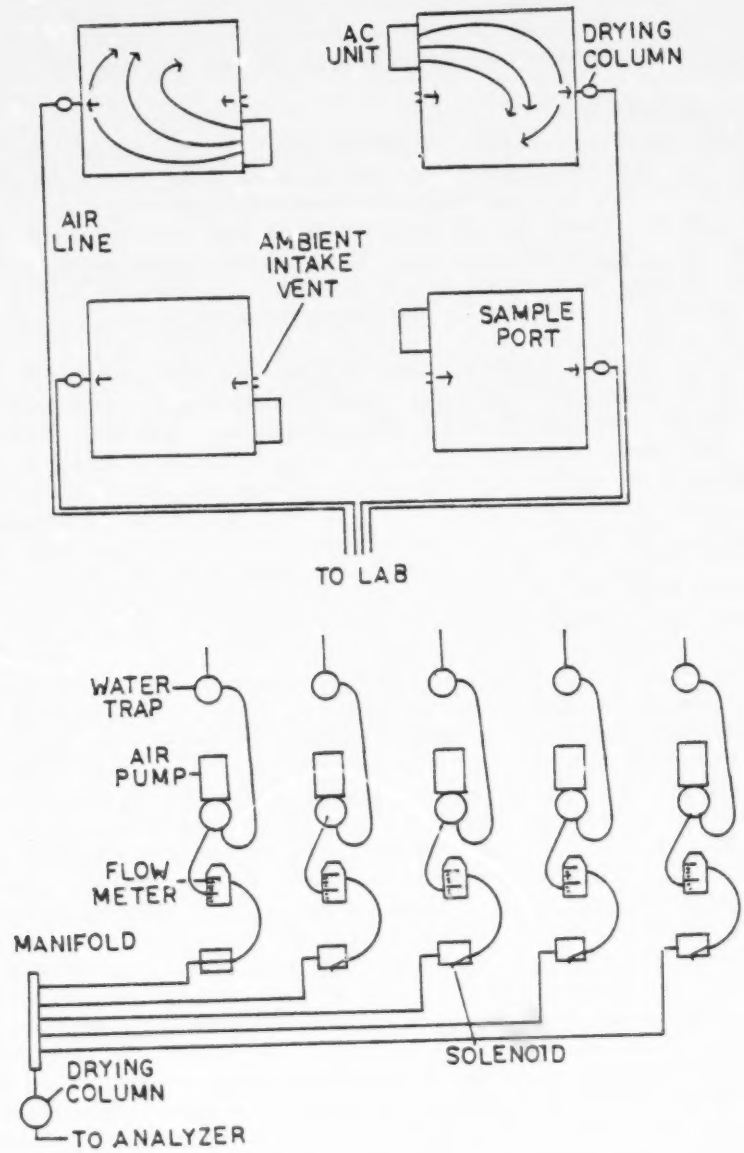

Figure 11. Schematic of air sampling system.

croecosystem). Twenty-four random core samples were collected from the control site. Twelve samples were analyzed and twelve were used as replacement cores for the microecosystem replicates. A 50 cc syringe was utilized as a coring device and samples were seived (67 micron mesh). Numbers of species and individuals were normalized to ten centimeter square values.

Preliminary Results--

Validation Studies. Table 2 represents both a ranked species list for the control site and the microecosystem unit as well as an ANOVA of the species densities (individuals/m^2) and species diversity (Shannon-Wiener) between the samples taken at the control site and the microecosystems. The fiddler crab, Uca pugilator, and the polychaetes, Heteromastus filiformis and Nereis succinea, were clearly the dominant species in terms of numbers of individuals per m^2 in both the microecosystem samples and the control site.

These three species were encountered in all the samples for both sites for all the time periods. The other species were only sporadically encountered although the relative abundances between the two sites remained essentially the same. Inspection of the ANOVA tables (Table 2) reveals that the communities within the microecosystems and the control site were not statistically different at the 0.05 level, in terms of species densities, with overall mean values of 114 individuals/m^2 for the control site and 174 individuals/m^2 within the microecosystems. The same results were found for the species diversities (Shannon-Wiener index) between the microecosystems ($\bar{H}$ = 0.57) and the control site ($\bar{H}$ = 0.52).

The results of the meiobenthic survey contrasting the microecosystems with control site are summarized in Table 3. Again in terms of total species densities the two sites are not statistically different at the 0.05 level with a mean value of 525 individuals/10 cm^2 for the control site and 352 individuals/10 cm^2 for the microecosystems. However, examination of the samples indicated a species composition shift in the microecosystem units over time. Initially, both the control site and microecosystem were dominated by copepod species. With time, nematode species became dominant while the Harpacticoid copepod species numbers declined. This observation led to an experiment begun in April 1976 and carried through for 30 days wherein a nektonic component (Palaemonetes vulgaris) was added to a flow-through refuge resevoir in the drain end of one of the tanks. Upon inundation during flood tides, the Palaemonetes (approximately 100 individuals) would swim out of the tank for excursion out over the substrate, presumably selectively feeding on the larger meiobenthos (the nematodes). This conjecture was based upon the findings of Sikora (personal communication) that nematodes comprised a major fraction of the gut content of Palaemonetes sp. Prodigiously, the Palaemonetes found their way back into the refuge resevoir (Fig. 10) during the ebbing of the waters in the microecosystems. The results of this experiment reported elsewhere (Bell and Coull, in press) are summarized in Table 3 as factorial ANOVA. Inspection of the ANOVA prior to the addition of the Palaemonetes indicates no significant differences between the microecosystems at the 0.05 level for any of the meiofaunal components. Time was a significant factor and probably represents some temporal succession within the units. After the addition of the Palaemonetes, there was a significant difference ($D \leq .05$) between the control (no

TABLE 2 MACROFAUNA

Species Listed in Order of Abundance

Control Site	Microecosystem
Uca pugilator	*Uca pugilator*
Heteromastus filiformis	*Heteromastus filiformis*
Nereis succinea	*Nereis succinea*
Uca pugnax	*Uca pugnax*
Geukensia dimissa	*Melampus bidentatus*
Melampus bidentatus	*Corophium* sp.
Orchestia grillus	*Orchestia grillus*
	Insects

ANOVA for Species Density (June 1976 - Feb. 1977)

	df	ss	ms	F
Treatment	1	40.04	40.04	2.95
Error	22	298.58	13.57	
Total	23	338.62		F.05(1,22)= 4.30

ANOVA for Species Diversity (June 1976 - Feb. 1977)

	df	ss	ms	F
Treatment	1	0.01	0.01	0.05
Error	22	4.02	0.18	
Total	23	4.03		F.05(1,22)= 4.30

Treatments were control site samples vs. microecosystems samples

TABLE 3 TOTAL MEIOFAUNAL DENSITIES BETWEEN MICROECOSYSTEM AND CONTROL SITE

ANOVA for (July 1976 - May 1977)

	df	ss	ms	F
Treatment	1	3001	3001	0.08
Error	69	261596	37912	
Total	70	2618963		F.05(1,69) = 3.98

Prior to Adding Shrimp (July 1976-March 1977)
Mixed Model ANOVA, To Test for Microecosystem Replicability and Time (n = 86)

		F_S				
Source of Variation	df	Total Meiofauna	Nematodes	Polychaetes	Oligochaetes	Copepods
Microecosystem	3	1.27	1.23	1.89	0.11	0.60
Time	6	4.50**	3.74*	8.95**	18.36***	13.5**
Interaction	18	0.89	1.10	1.04	0.31	0.56

After Adding Shrimp (4 April-25 May 1977)
Model 1 ANOVA, To Test for Shrimp Effect (n = 18)

		F_S				
Source of Variation	df	Total Meiofauna	Nematodes	Polychaetes	Oligochaetes	Copepods
Microecosystem	1	9.96**	10.67**	10.53**	7.40*	2.99
Time	2	2.08	0.24	1.66	2.58	3.52
Interaction	2	0.13	0.60	1.19	4.81*	0.05

*Significant at P < 0.05
**Significant at P < 0.01
***Significant at P < 0.001

Palaemonetes) and the test (Palaemonetes added) microecosystem. The shift in species composition approximated the composition at the control site when the study was ended.

Nutrient Fluxes and Community Metabolism--

In the following section we have presented an example of a nutrient budget and community metabolism determination. The data are intended only to demonstrate the type of data that may be obtained utilizing our experimental design. Comprehensive evaluations will follow in subsequent papers.

Net fluxes of nutrients were determined by comparing areas under rate change curves plotted for flood and ebb components of the tide. Water samples from the input line and each outflow drain were collected every fifteen minutes for the nutrient determinations as depicted in Figure 12. The flow rate at each location was recorded, along with the date and time. By using standard analytical techniques (Strickland and Parsons, 1972), concentrations of the following nutrients were determined: nitrates, nitrites, ammonia, total phosphorous; and reactive phosphate phosphorous concentration and flow values were then used to calculate the nutrient flux rate at each sampling interval. Rate change curves were plotted for the inflow and outflow of each tank over the sampling period (Fig. 12). The curves were integrated, with a comparison of the areas under the curves, yielding net values for import or export of each nutrient in each tank. In this particular example, 24 mg of total phosphorous was imported into the microecosystems; 0.1 mg of reactive phosphorous was exported; 11 mg of total nitrogen was exported; 0.7 mg of nitrate nitrogen was exported; and 15 mg of ammonia nitrogen was imported. We do not have enough data to make a comprehensive statement regarding these fluxes at this time. However, the trend of the total phosphorous import was observed in every instance.

A similar, but more complicated method was used to determine community metabolism or primary productivity. The average rate of change in the mass of carbon in the enclosed air was determined in hourly increments in the example provided (Fig. 13). These values were then corrected for changes caused by net fluxes of carbon due to the flow-through air design. Negative rates indicate net production and positive values show net respiration. The corrected values were then used to plot rate change curves for the sampling period. Comparisons of the integrated curves were then made to find net photosynthesis/respiration (P/R) ratios for each tank. An example set of curves are illustrated in Figure 6. In this particular example, net photosynthesis ranged between 0.14 $gC/m^2/day$ to 0.20 $gC/m^2/day$ for the four replicate microecosystems. Respiration values ranged between 0.12 $gC/m^2/day$ to 0.16 $gC/m^2/day$. One would expect some variations in these absolute values due to slight discrepancies in the experimental conditions within each unit. The P/R ratio normalizes these values and the values recorded for the four replicates varied only between 1.1 and 1.2

CONCLUDING REMARKS

We feel we have accomplished the design and initial testing of a viable and functional microecosystem or "living" model of a selected salt marsh community. This model seems to simulate the natural marsh in terms of its

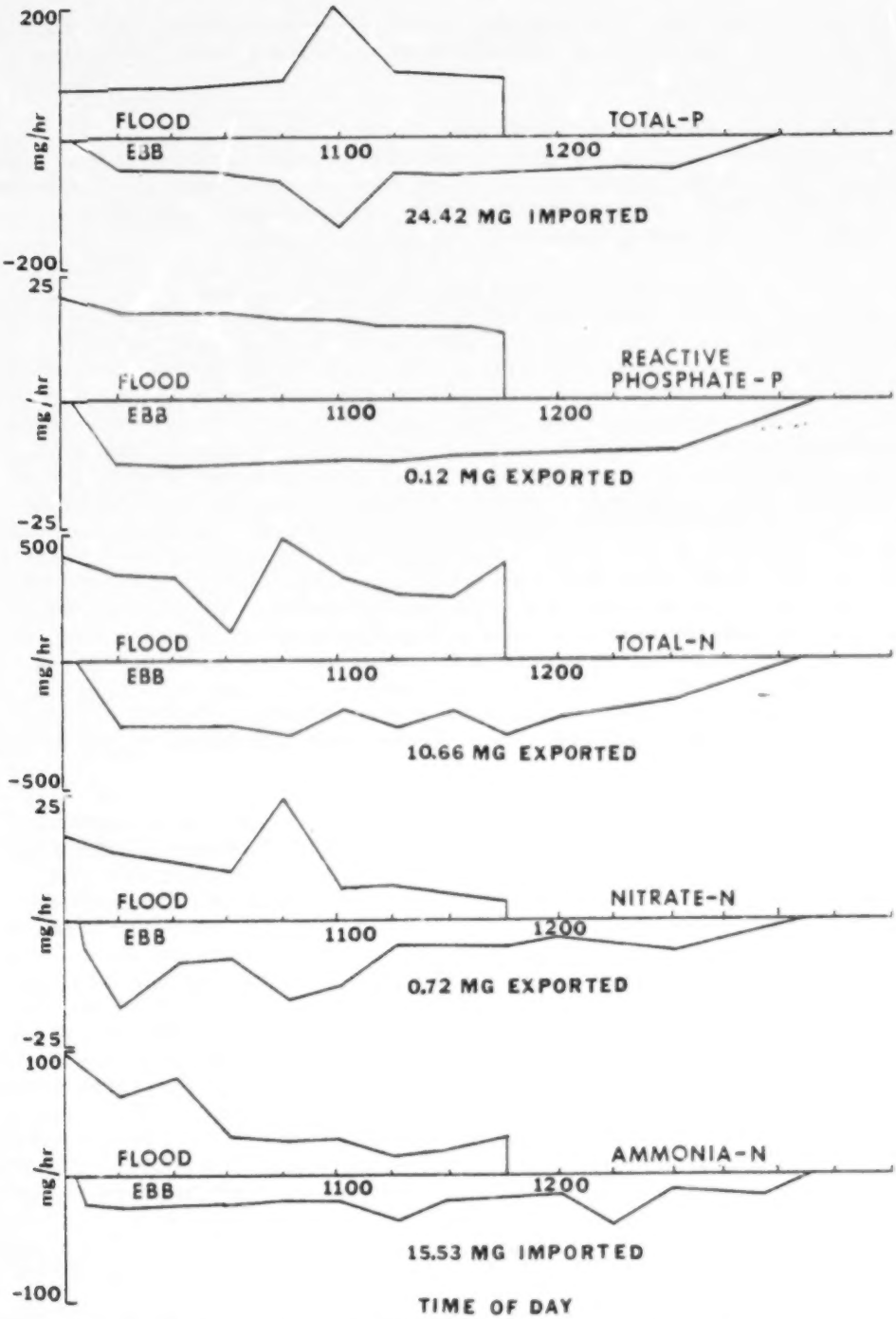

Figure 12. Exemplary nutrient flux curves.

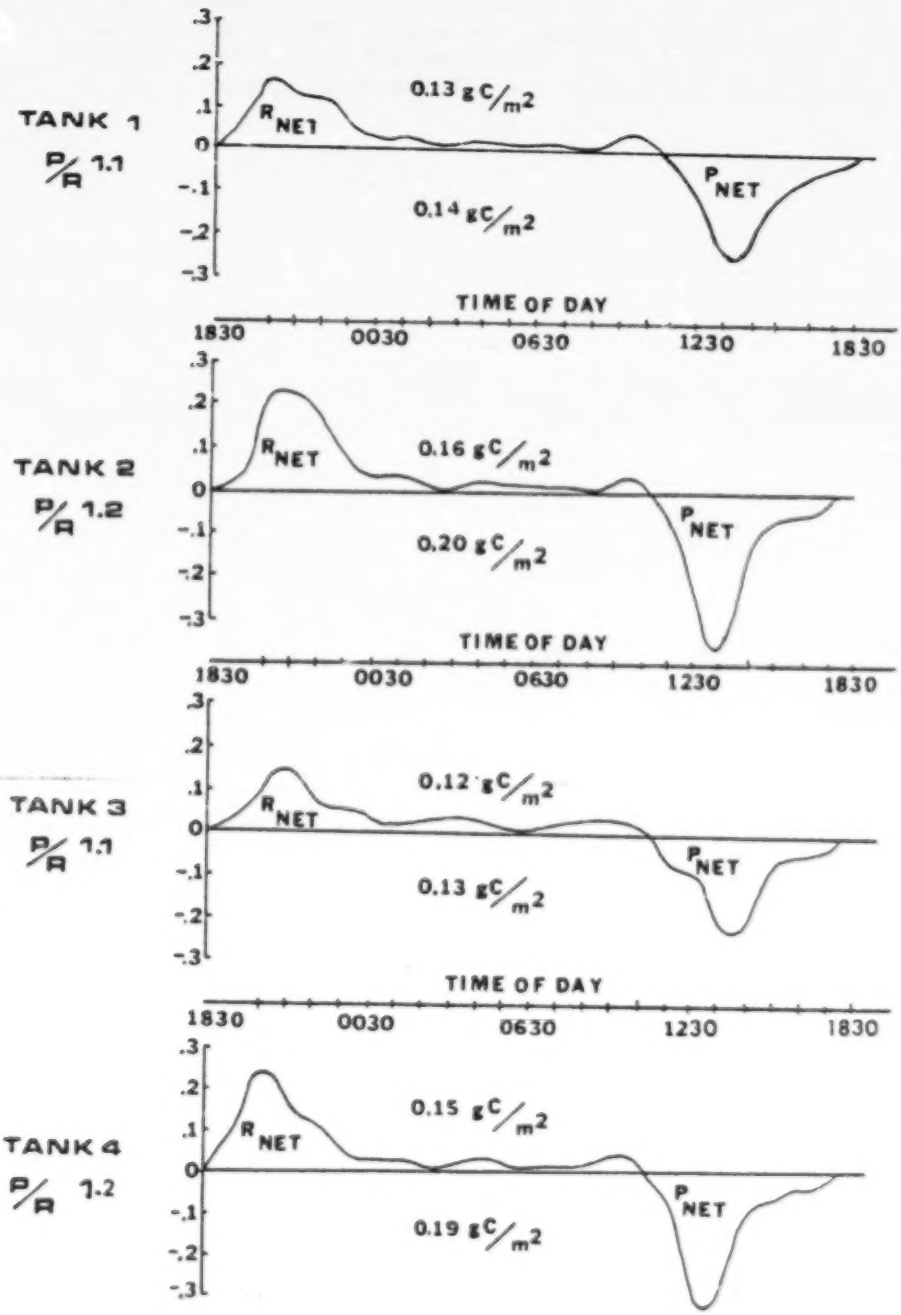

Figure 13. Exemplary community metabolism curves.

of its structural components. Tests related to certain functional aspects such as nutrient assimilation and community metabolism between the model and natural marsh should further validate the model. This design should be a potentially valuable tool for the assessment and prediction of certain environmental perturbations within the salt marsh ecosystem.

SECTION 7

SUMMARY OF REPORT

F. J. Vernberg

This report represents the results of the third-year study of what was to be a five-year investigation of a relatively undisturbed estuary-marshland ecosystem, the North Inlet Estuary, Georgetown, South Carolina. A summary of the first two years' work has been published in the Ecological Research Series (EPA-600/3-77-016, January 1977).

The overall objectives of the planned five-year study were modified in response to a reduced level of funding. Two substudies were undertaken. 1) update of the macroecosystem model of the North Inlet Estuary; and 2) continuing development of an experimental microecosystem.

A non-linear, deterministic model of the interactions within and between the Spartina salt marsh and the estuarine water mass has been proposed and simulated. Preliminary simulation results show that the modeled system is stable and produces seasonal changes in simulated parameters which resemble measured fluctuations in Spartina-dominated estuaries. Whether or not these simulated trends in metabolism, biomass, and export are actually characteristic of the North Inlet estuary will be determined by continued data analysis and collection. Regardless of the present validity of the model it represents the status of our understanding of the North Inlet marsh-estuarine ecosystem with its complex interactions of physical, geochemical, and biological processes.

A viable and functional microecosystem or "living" model of a selected salt marsh community has been designed and tested. This model seems to simulate the natural marsh in terms of its structural components, and testing certain functional aspects, such as nutrient assimilation and community metabolism between the model and natural marsh, would further validate the model.

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